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Volume 6 1959

Published by the
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The University of Texas
Port Aransas, Texas

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INSTITUTE OF MARINE SCIENCE
THE UNIVERSITY OF TEXAS
PORT ARANSAS, TEXAS

The Institute of Marine Science with laboratories at Port Aransas, Texas is a research division of The University of Texas related to the Departments of Bacteriology, Botany, Chemistry, Geology, Physics, and Zoology and the Meteorology Division of the Department of Aeronautical Engineering at the Main University at Austin. An integrated teaching program in graduate marine science is made up of the course offerings from the several departments and from the Institute.

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Alacran Reef, Campeche Bank, Mexico

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Abstract

A geological study was made of the Alacran Reef, a complex of living coral reefs situated on the Campeche Bank north of the Yucatan Peninsula. The paper contains a map showing the distribution and bathymetry of reef zones; profiles of the reef outer slope, reef front, lagoon, and area between the mainland and the reef; analyses of typical reef sediments; photographs of characteristic reef features; and a list of reef corals, mollusks, and other invertebrates. The reef has the form of an atoll, with a central "lagoon" having a maximum depth of about 75 feet. The reef outer slope rises from a water depth of about 160 feet to 20–50 feet where there is a marked decrease in slope. The decrease in slope approximately coincides with the depth of a sharp break in the slope on the Campeche Bank between Progreso and the reef which suggests that they may have a common origin; possibly both are the result of marine erosion during a low stand of the sea during the Pleistocene. The arcuate shape and

northwesterly orientation of the Alacran Reef results from its being in the northeast trade wind belt. Alacran Reef as a whole is probably in an earlier phase of development than all the rest of the reefs of the Campeche Bank and the reefs of Veracruz and Anton Lizardo.

Introduction

Alacran Reef is a complex of coral reefs located about 70 miles north of the port of Progreso, Yucatan, Mexico, and about 30 miles south of the scarp forming the northern edge of the Campeche Bank (Figure 1). Alacran Reef is larger than three other coral reefs Cayo Arcas, Triangulos, and Cayo Arenas situated near the bank edge east and south of Alacran Reef. It is the only reef along the Mexican coast having a topographic feature that resembles a lagoon.

The reefs of the Campeche Bank seem to have received less scientific attention than other reefs in the world, *e.g.*, the fairly comprehensive bibliography of organic reefs, bioherms, and biostromes compiled by the Seismograph Service Corporation and edited by W. E. Pugh (1950) contains no references to the reefs of the Campeche Bank. Alacran Reef was visited in 1878 by Alexander Agassiz (1879), who briefly described the reef in a letter written to C. P. Patterson, Superintendent U.S. Coast Survey, Washington, D.C. Agassiz (1888) described the reef in more detail in Volume 1 of "Three Cruises of the United Coast and Geodetic Survey Steamer 'Blake'."

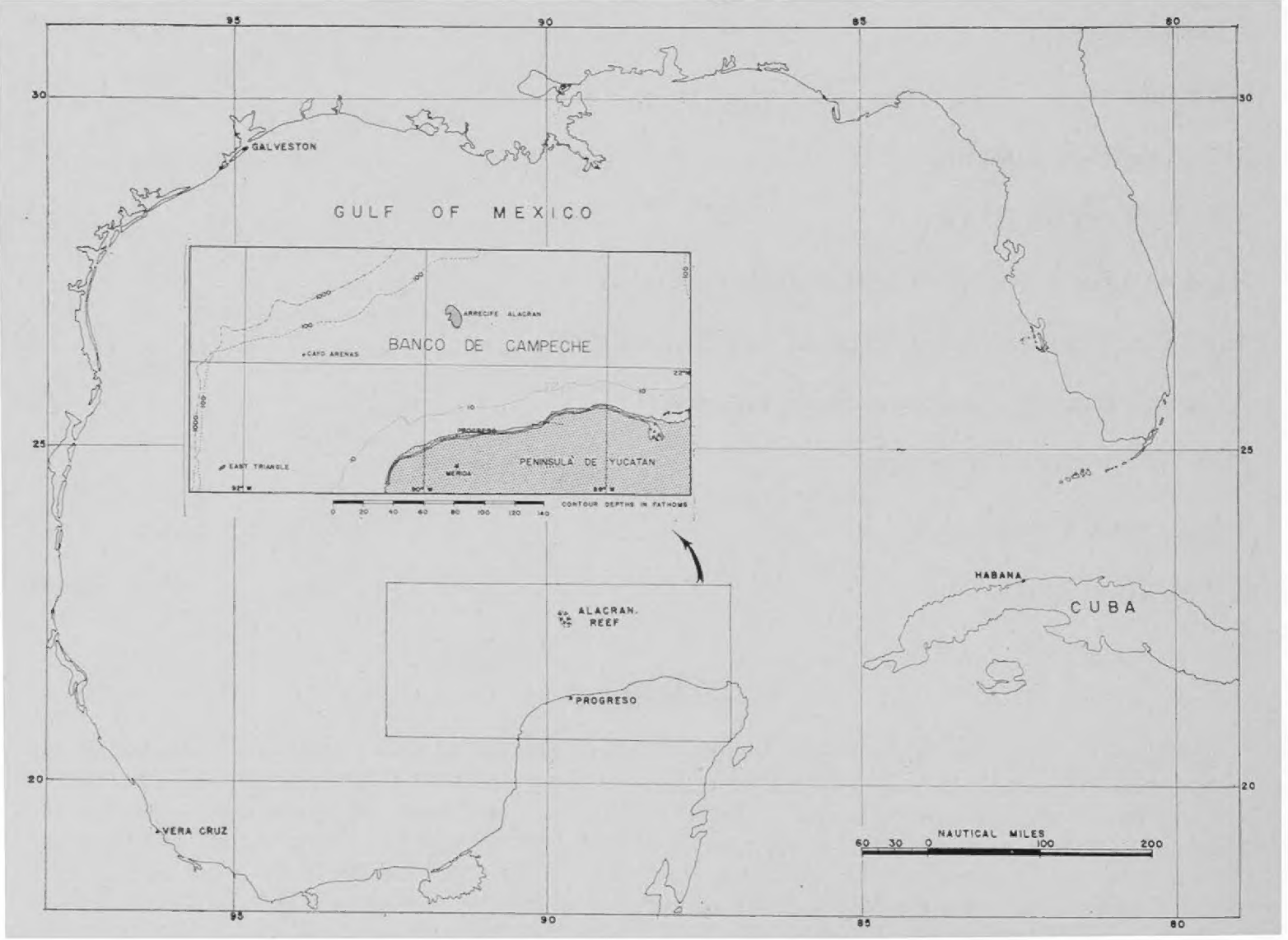

FIG. 1. Map showing location of the Alacran Reef. Bathymetry in the vicinity of Alacran Reef is shown on Chart 1290, 1942, of the United States Hydrographic Office.

Present day areas where carbonates are being deposited hold considerable interest for geologists principally because of the abundance of carbonate rock in the geologic record (Le Blanc and Breeding, 1957). The Campeche Bank may afford sedimentary conditions more like the widespread carbonate shelves of earlier geologic times than the Bahama Banks which are completely isolated from the continent, or Florida Bay whose sediments seem unique in many respects (F. Lozo, written communication, 1957).

The writers are participants in a scientific investigation of the geology and biology of Alacran Reef and surrounding waters sponsored by the Instituto de Geologia of Mexico. The present contribution, resulting from field work on the reef during June, 1959, consists of a map of the reef prepared on a photogrammetric base, fathometric profiles across the reef and between the reef and the mainland, and a general description of the reef.

Acknowledgments

This work was financed by grant number NSF-G 8902 from the National Science Foundation. Field work on the Alacran Reef would not have been possible without the groundwork laid by Ing. Guillermo P. Salas, Director, Instituto de Geologia, Mexico. We are most appreciative of the tireless efforts of Director Salas in behalf of the investigators taking part in the expedition.

The present contribution concerning the submarine topography of the reef was helped considerably by the able assistance of Ing. Amado Yañez of the Instituto de Geologia, and by the loan of a fathometer by this Institute when our instrument was in need of repair. Dr. Robert L. Folk, who is studying the processes involved in the formation of the sand islands of the reef, gave us a clearer picture of sedimentary processes at work on the reef.

Other participants whose work contributed to the success of the expedition were Dr. Henry Hildebrand; Ing. Humberto Chavez; Ing. Julio Monges; Ing. Carlos Cañon Amara; Ing.Rafael Marquez C.; Sr. C. Duran; Sr. A. Arias; Sr. R. Bravo; Sr. A. Diaz; and Messrs. J. Dan Powell, Henry Compton and Thomas Wright. Of special note was the help of Captain J. Lezama and Lieutenant J. Becerril, of the Mexican Navy, whose understanding of the problems involved and interest made the operation move smoothly and swiftly. We are also appreciative of the hospitality and assistance received from C. Lic. Joaquin R. De LaGala, C. Administrador de la Aduana in Progreso, and personnel of the Mexican Government stationed on the island of Perez, especially Sr. Cándido Sánchez Cabañas and Lieutenant Gorge E. Roff. Much of the logistical work on the Yucatan Peninsula was done by Sr. F. Javier Campos, Jr. and Sr. F. Javier Campos, Sr. whose assistance was invaluable. Mr. Charles D. Wise has reviewed the manuscript and assisted with basic logistics.

The field work of Charles M. Hoskin was partly supported by an award from the National Research Council, Foreign Field Research Program. The analyses of sediments presented in this paper were made by Mr. Hoskin preliminary to a comprehensive study of the submarine sediments of Alacran Reef for a dissertation in geology at The University of Texas. Dr. Henry Hildebrand is studying the fish and crustaceans of Alacran Reef and collected some of the octacorals reported in this paper. The octacorals were

identified by Dr. F. M. Bayer through the courtesy of Dr. Fenner A. Chase and the United States National Museum.

We are very grateful for criticism of the manuscript by Dr. Henry Hildebrand, Dr. John Imbrie, Dr. Robert L. Folk, and Dr. Harry S. Ladd.

The Campeche Bank

The Yucatan Peninsula separates the Gulf of Mexico on the north and west from the Antillean Sea on the east. The land is low-lying, under 650 feet in height, and is made of Tertiary limestone with karst topography. The country is almost devoid of rivers. The peninsula extends out under the gulf for an average distance of about 125 miles to form the Campeche Bank and then descends abruptly into the deep water of the gulf (Schuchert, 1935).

The origin of the escarpment bounding the Campeche Bank has not been established with certainty. A long held theory of faulting (Schuchert, 1935 and Alvarez, 1949) has recently been challenged by Miller and Ewing (1956) who conclude from magnetic measurements made on the northern edge that scarps bounding the Campeche Bank are not tectonic. According to Miller and Ewing (1956), the observed magnetic anomalies can be accounted for if the edges of the Campeche Bank are formed on a row of basaltic volcanoes which subsided as lime formed; a similar origin was suggested for the eastern edge of the Bahamas. Newell (1955) concluded that the Bahama rim escarpment is the front of a drowned barrier reef, probably of late Tertiary age. It is not unlikely that the Campeche Bank escarpment has a similar history. It may be mentioned in this connection that in two deep corings made by Petroleos Mexicanos (Sacapuc and Chicxulub) near Progreso, Yucatan; an andesitic flow has been found under a thick sequence of Tertiary sediments (Sansores, 1959).

A series of bottom profiles was constructed from the records of a Bendix 0-300 foot depth recorder. A profile between Alacran Reef and Progreso, Yucatan (Figure 2) shows that the bottom slopes sharply away from land to a depth of approximately 40 feet and then the slope decreases and remains fairly constant for the remaining distance to Alacran Reef. The depth of the sharp break in slope approximately coincides with the lower edge of the reef front (Figure 3, A-J) which suggests that they may have a

FIG. 2. Bottom profile between Progreso, Yucatan, and Alacran Reef.

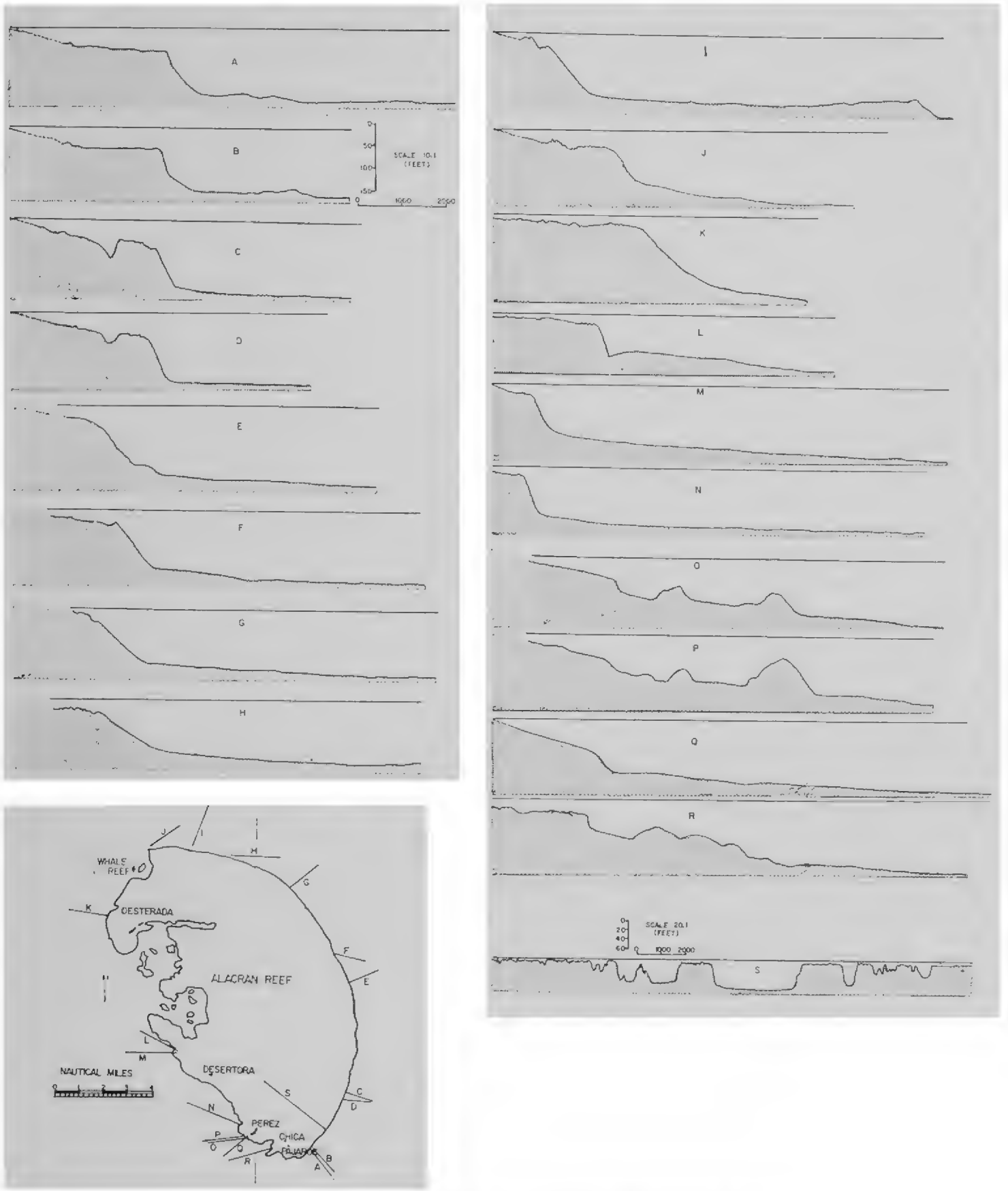

FIG. 3. Bottom profiles at Alacran Reef and location map.

common origin; possibly both are the result of marine erosion during a low stand of the sea during the Pleistocene. The bottom between Progreso and Alacran Reef has minor depressions and prominences which seem more abundant at about 75 feet depth. These may be remnants of karst topography formed during exposure of the Campeche Bank during some glacial period. Sampling over a prominence using a Van Veen dredge indicated a rock bottom. Several profiles made between Progreso and the reef indicated that the strip containing many prominences and depressions was more or less

linear and paralleled the coast. Sediments were absent over much of the bottom between Progreso and the reef. Where present, the sediment consisted of bioclastic, well-sorted, medium to fine grained carbonate sand. The strong water currents between Progreso and the Alacran Reef probably exert a winnowing action on bottom sediments.

The Campeche Bank is in the northeast tradewind belt. These winds probably account for the arcuate shape and orientation of Alacran Reef. Year-round westward moving water currents across the Campeche Bank probably also influence the shape and orientation of the reef.

Alacran Reef Outer Slope and Reef Front

The outer slope is the steeply descending part of the reef below the dwindle point of abundant living coral and coralline algae (Tracey, Cloud, and Emery, 1955). The upper margin of the outer slope of Alacran Reef is marked by an abrupt decrease in slope at 30 to 50 feet depth on the windward side of the reef and somewhat shallower on the lee side, 20 to 30 feet depth (Figure 3). On the windward side of the reef the outer range of *Acropora palmata* approximately coincides with the upper margin of the outer slope.

FIG. 5. Proliferous growth of soft, encrusting coral coating overhanging ledge in shallow water of inner edge of reef near Pajaros.

FIG. 6. Typical growth of *Acropora palmata* on the southern end of reef near Pajaros.

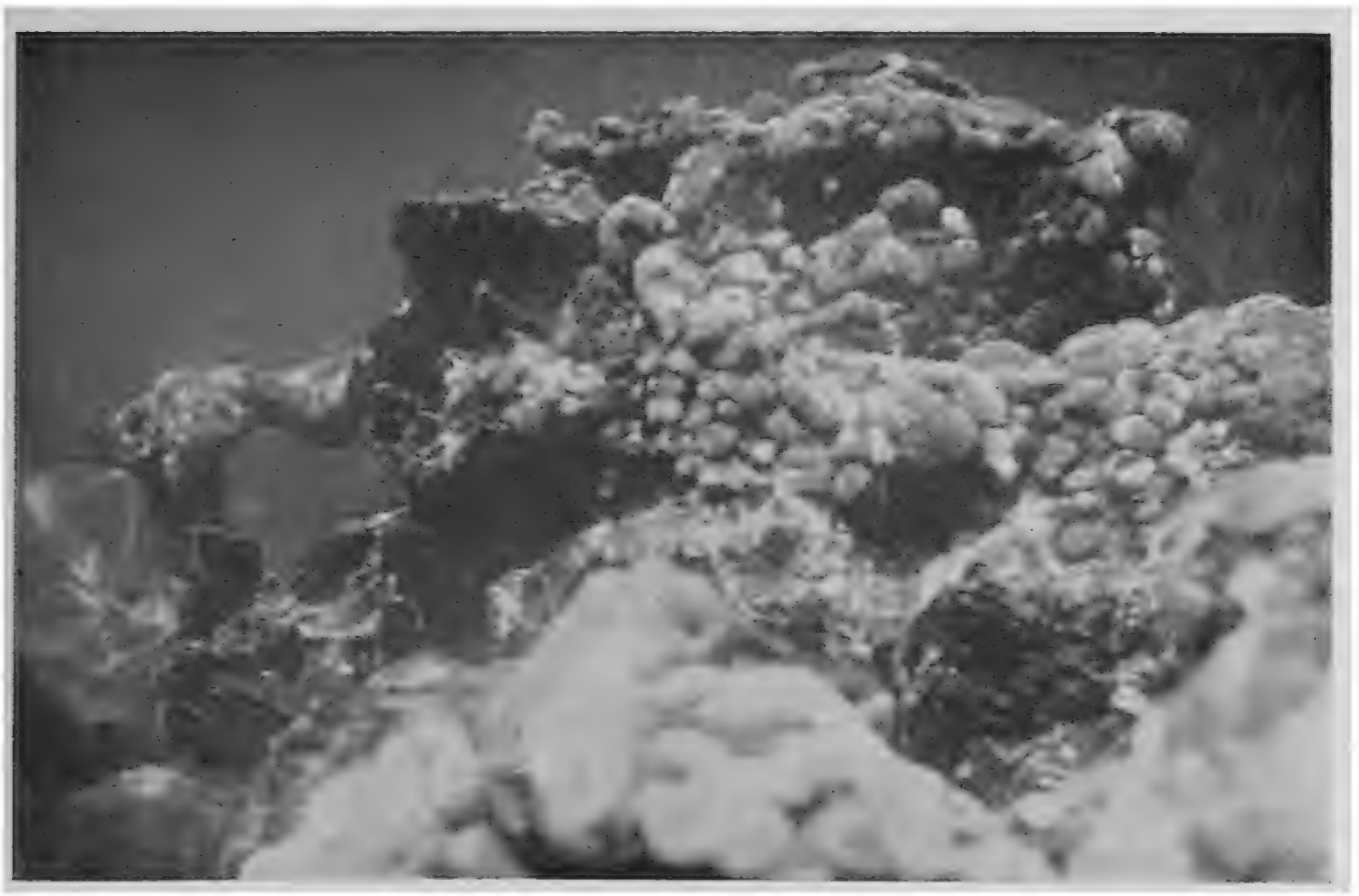

FIG. 7. Natural bridge in reef caused by erosion or coral overgrowth. Sea fan is obscure in left foreground. Soft, encrusting corals coat reef rock.

Because of the clarity of the water it was possible to make observations of the bottom from the water surface in water 90 feet deep. At this depth a large part of the bottom consists of open sand areas, and the only corals observed were massive types. At a 60 foot depth, which is considered the upper part of the outer slope, massive corals, sea pens, and sea whips are abundant and a low algal growth covers about 50 per cent of the bottom. The sea floor at the base of the outer slope is at a depth of approximately 160 feet. In general, the outer slope is more gentle at the lower part, probably as a result of talus accumulation. On the sea floor out from the outer slope, local topographic rises probably represent embryo reefs which are not living at the present time (Figure 3, L).

The reef front is the upper seaward face of the reef, extending above the dwindle point of abundant living coral and coralline algae to the reef edge (Tracey, Cloud, and Emery, 1955). The reef front of the Alacran Reef includes a shelf up to three-quarters of a mile wide. On the windward side of the reef the inner limit of the shelf might be considered as the intertidal zone. On the lee side of the reef the inner margin of the shelf is the lagoon because here the reef edge is below water (Figure 4). Zones of organic life more or less parallel the windward side of the reef. Below the intertidal zone in about four feet of water *Acropora palmata* is common but an encrusting soft coral is the dominant organism (Figure 5). *Acropora palmata* becomes dominant in about 15 feet of water and then decreases in abundance disappearing at the upper edge of the outer slope (Figure 6). Gorgonians are common from the intertidal zone (Figure 7) to about 45 feet water depth. Massive corals including *Diploria* and *Montastrea* are abundant on the shelf. *Millepora* was observed down to about 45 feet water depth. *Halimeda* is extremely abundant especially in the shallower part of the shelf.

The shelf on the lee side of Alacran Reef contains patch reefs that almost reach the surface in water as deep as 14 feet but dwindle in deeper water. Beds of *Thalassia* and *Sargassum* cover much of the bottom. *Acropora palmata, Diploria* and *Montastrea, Gorgonia, Millepora,* and sea whips are abundant on the patch reefs. *Acropora palmata* which grows in a stunted condition on Alacran Reef, is scarce on the bottom between the reefs. Rock ledges two feet or more in height are quite common on the lee shelf. The windward shelf sediments are very coarse sands and gravels composed mostly of *Acropora* fragments, mollusk hash, Foraminifera, and *Halimeda* plates (Table 1 and Figure 8). The leeward shelf sediments contain similar components but are finer with a smaller component of *Acropora* fragments and a greater component of Foraminifera tests. Reef front grooves running perpendicular to the reef edge were observed along the northern part of the windward upper shelf.

An interesting topographic feature at Alacran are "ridges" around the southern end of the reef, both on the windward side (Figure 3, C and D) and lee side (Figure 3, O and P). These ridges have their tops almost at the same level as the deeper part of the lagoon and with the bottom of the marginal channel. These features may be the remnants of a platform cut by waves during a low stand of the sea.

Alacran Reef Seaward Margin and Reef Flat

The seaward reef margin is the seaward edge of the reef flat (Tracey, Cloud, and Emery, 1955). The windward edge of the Alacran Reef is marked by breakers and is

TABLE 1

Composition and descriptive parameters of Alacran Reef sediments[a]

	Sediment from windward reef front	Sediment from windward reef flat	Sediment from *Thalassia* patch on inner reef flat	Sediment from lagoon bottom at 65 feet water depth	Sediment from central depression at a lagoon patch reef
Composition %					
Halimeda	50.0	17.8	33.6	10.5	36.6
Mollusks	13.8	19.3	25.4	31.0	16.5
Coral	16.8	25.1	26.2	14.5	20.3
Foraminifera	16.2	22.0	7.9	21.0	14.6
Coralline algae	1.2	4.6	2.2	9.4	3.9
Ostracodes	.....	1.0	0.7	6.3	0.7
Spicules	0.6	5.4	1.5	5.8	1.9
Sediment Parameters					
Mean grain size					
Phi (-log$_2$ diam.)	0.07	1.33	0.87	4.08	— 0.58
mm	1.05	0.40	0.56	0.06	1.55
Grain size name	Very coarse sand	Medium sand	Coarse sand	Coarse silt	Very coarse sand
Inclusive Graphic standard deviation[b]	1.32 Poorly sorted	0.92 Moderately poorly sorted	1.39 Poorly sorted	0.70 Moderately sorted	1.39 Poorly sorted
Inclusive Graphic skewness†	0.40 Strongly fine skewed	0.01 Nearly symmetrical	— 0.30 Coarse skewed	— 0.74 Strongly coarse skewed	0.86 Strongly fine skewed

[a] Table 1 is solely the work of Charles M. Hoskin.
[b] See Folk, R. L., and Ward, W. C., 1957, Brazos River bar: a study in the significance of grain size parameters: Jour. Sed. Pet., 27, 3–26.

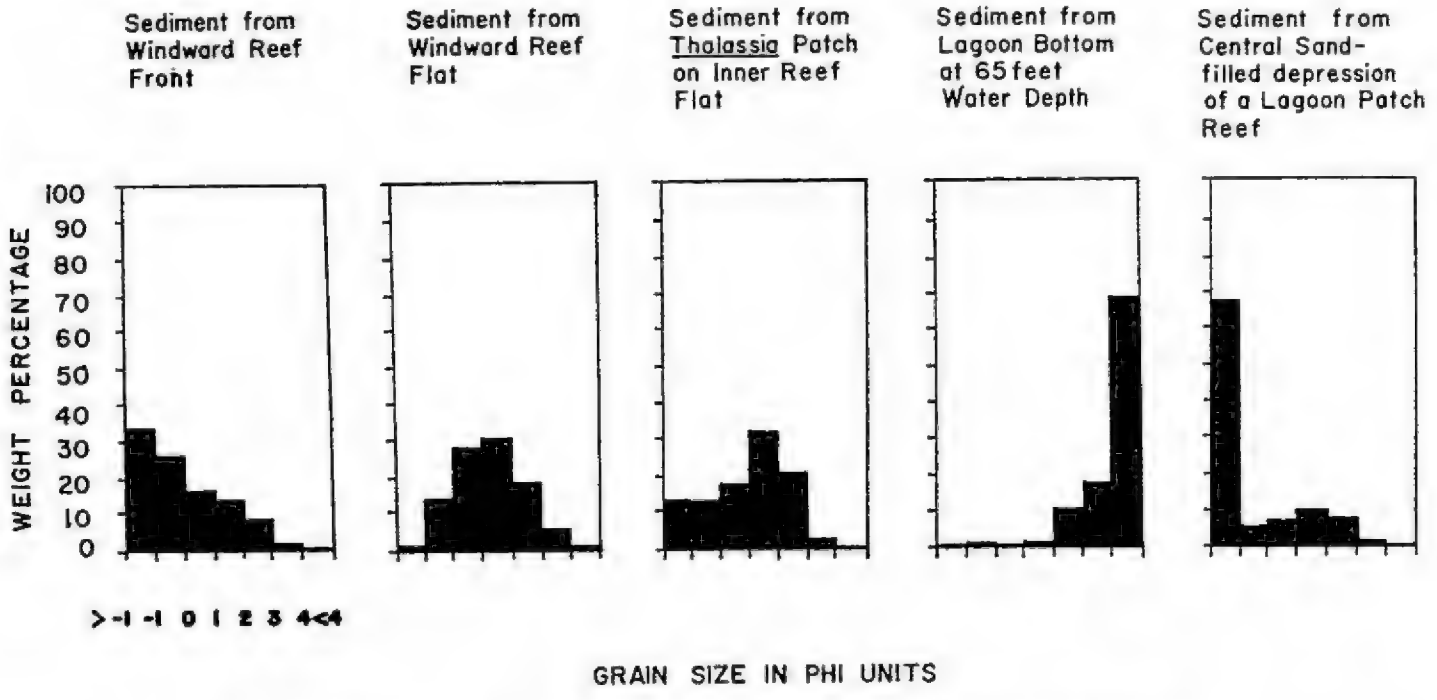

FIG. 8. Histograms showing the size distribution of selected sediments.

above water at low tide. No distinct coralline lip was noted, but a coralline alga, probably *Porolithon*, coated rocks and shells at, and immediately below, the water surface. Two major surge channels break the reef front. Investigation of the northernmost channel with an aqualung provided the following detailed description of this channel:

The channel begins on the slightly submerged reef flat as a broad, more or less triangular, depression with the apex of the triangle toward the reef front. The depression

narrows and steepens until what might be termed the head of a "canyon" is reached where the width of the canyon floor is about 60 feet (Figure 9). The walls here slope downward from the reef flat at an angle of about 20° to the floor which lies in about 36 feet of water. The walls have lateral projections formed by coral growth. The canyon narrows seaward to a width of about 30 feet and the walls become steeper, finally becoming vertical at the seaward reef margin. The floor of the canyon slopes downward in an undulating fashion, and is covered with coarse, white calcareous sand and blocks of reef rock (Figure 10). In places these blocks are so large that they almost close the canyon at the floor. Turbulence created by these large blocks in the currents flowing through the canyon may cause the undulations in the canyon floor. At the seaward reef margin the canyon seems to widen, probably fanning out to merge with the outer shelf. Numerous caves and tributary channels may be seen cutting back into the vertical sides of the canyon. Exploration of one of these caves revealed several large holes in the roof through which daylight streamed. The caves seem to be formed by the growth of coral over tributary channels, the roof holes being places which have not yet been overgrown.

The windward edge of the reef is marked by an accumulation of coral boulders two feet and more in diameter. These boulders are covered with encrusting soft coral below the intertidal zone. Massive corals, *Acropora palmata*, *Millepora*, *Gorgonia*, and *Halimeda*, are abundant below low tide level. The mollusks *Littorina ziczac* and *Nodilittorina tuberculata* were collected in the intertidal zone near the reef edge from marble blocks which had been the cargo of a ship wrecked on the reef.

The reef flat behind the seaward reef margin contains considerable coral rubble. Coral boulders one to three feet in diameter are abundant and spaced at one foot intervals or less. Larger boulders are scattered over the reef flat (Figure 11). The coral rubble is principally composed of worn fragments of *Acropora*. The boulders are not nearly so abundant as in other reefs of the gulf, for instance in Arrecife de Enmedio (Anton Lizardo group). The coral rubble is principally composed of worn fragments

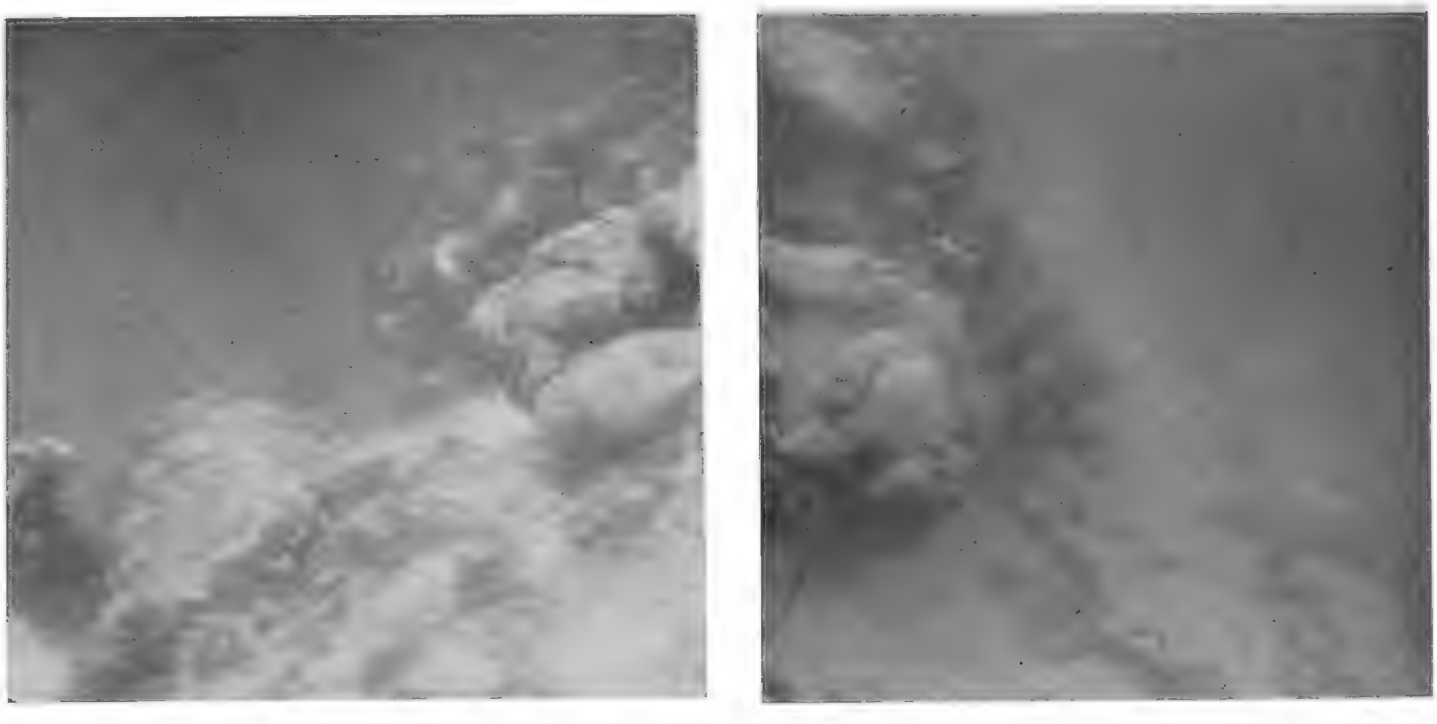

FIG. 9. Wall at head of the canyon through reef front where water depth is about 36 feet.

FIG. 10. Canyon head where wall and bottom meet in about 36 feet of water.

FIG. 11. Reef flat behind seaward reef margin at low tide with water less than one foot in depth. Rubble about one foot in length is exposed in the lower part of photograph and boulders are exposed in the upper part.

of *Acropora*. Sea urchins, the snails *Asteraea* and *Strombus*, and the alga *Halimeda* are common on the reef flat. Many of the coral fragments and rubble are coated by a moss-like alga and coralline alga (*Porolithon?*). Coralline algae are not as abundant on the reef flat at Alacran as on the Veracruz and Anton Lizardo reefs. The algae *Sargassum* and *Turbinaria* were observed on the reef flat but they may have been recently washed over from the reef front. Sand on the reef flat is medium to coarse in size and consists of tabular flakes of mollusk shells, *Halimeda*, Foraminifera, and fragments of coral. A reef flat is essentially absent from the lee side of Alacran Reef. The reef flat near Chica is cut by narrow channels (Figure 12).

A discontinuous channel varying considerably in width and depth lies behind the outer reef flat and parallels the seaward reef edge. The channel is missing from most areas but in places it is a major topographic feature, 1000 feet wide and 42 feet deep. Spot sediment sampling indicates that the bottom of the channel contains only a thin veneer of sand. Patch reefs and pinnacles of coral project upward from the channel bottom.

The inner reef flat is considered as the area bounded on its outer side by the reef flat channel or outer reef flat, where the channel is missing, and on the inner side by the lagoon. An inner reef flat is not present on the lee side of the lagoon. The lagoonal boundary of the inner reef flat is poorly defined but in the accompanying map (Figure 4 inside of back cover) it is marked by an increase in the area covered by water deeper than that found on the reef flat. The inner reef flat is shallow with the water usually less

FIG. 12. Channel in reef flat at southern end of reef near Chica. Grouper is about one foot in height. Channel wall is covered with a proliferous growth of *Millepora*.

than six feet deep. Patch reefs are extremely abundant. The inner reef flat at the northern end of the reef supports extensive beds of *Thalassia*. Sand in the *Thalassia* is coarse and composed principally of *Halimeda* plates, mollusk hash, and Foraminifera.

Alacran Reef Lagoon[1] and Sand Islands

The lagoon of Alacran Reef is well defined at its western boundary of the precipitous lagoon slope of the lee shelf whose inner edge lies in about 12 feet of water. The surface of the lagoon floor is undulating with maximum depth at about 75 feet. The east-central portion of the lagoon is partly filled by an anastomosing network of reef which is apparently filling in the lagoon, although visual inspection shows that living corals are found only in isolated patches. The main trend of the lagoonal reef network more or less

[1] The term lagoon is used for convenience and is not meant to suggest close relationship with lagoons of Pacific atolls.

parallels the longitudinal reef axis. As the upper edge lies close to the water surface, navigation in a shallow draft skiff across the lagoon is difficult, especially at low tide.

Every "pool" in the network as well as the lagoon as a whole, acts as a sediment trap, which is being filled in by the loose sediments abraded from the windward edge of the reef. The "pools" of the network are far shallower than the lagoon proper indicating that they are being filled more rapidly. As this "filling in" action proceeds, the reef flat will gain in extension at the expense of the lagoon so that the end result will be a leveling of all the surface of the reef and the complete obliteration of the lagoon, *i.e.*, its transformation into a typical table reef.

Prolific coral reefs grow along the lagoon reef margin off the island of Perez. Massive corals are dominant along the margin of one reef about 50 feet east of Perez (Figure 13), whereas *Acropora cervicornis* is dominant on the margin of an adjacent reef about 150 feet east of Perez (Figure 14). The outer slopes of both reefs descend steeply to the lagoon floor which is 25 to 35 feet deep along the slope base. The slope of the *Acropora* reef is covered with a tangled accumulation of *Acropora*. The prolific coral growth along the margins of these reefs occurs where the water is three to four feet deep. The shallow subtidal flats between the reef and the sand beach of Perez support *Thalassia, Halimeda, Porites furcata* (Figure 15), and isolated coral heads (Figure 16). Holes occupied by octopi are common on these flats and are marked by an accumulation of pebbles and disarticulated clam shells.

The subtidal area on the lagoon side of the islands is in many places covered with a pavement of fragments of *Acropora cervicornis* two to four inches in length. The inter-

FIG. 13. Inner edge of lagoon reef composed of massive corals east of Isla Perez. Large corals belong to the genus *Diploria*. Water depth is about three feet.

FIG. 14. Tangled accumulation of *Acropora cervicornis* on lagoonal reef adjacent to the islands of Perez. Water depth of photographed area is about 12 feet.

FIG. 15. *Thalassia* bed on lagoonal reef flat off east shore of Isla Perez. Plants in foreground are *Sargassum*. Water depth is about three feet.

FIG. 16. Massive corals on lagoonal reef flat east of Isla Perez.

tidal area, on the other hand, is usually sand with an abundance of *Halimeda* plates. If the lagoon reefs of Perez are considered typical of one type of lagoon reef margin, the area east of Desertora might be considered typical of another type. Here the bottom slopes gradually to where the water depth is about 22 feet and then slopes more sharply until a floor is reached at about 33 feet. Massive corals, sea fans, sea whips, the algae *Turbinaria* and *Penicillus,* and the hydrozoan *Millepora* occur as scattered growths on the shelf above the shelf margin with abundance greatest in water about seven feet deep.

Patch reefs are common in the lagoon. These rise sharply from the bottom and many almost break the water surface. The reef base often has a smaller diameter than the upper part (Figure 17). A typical patch reef is about 150 feet in diameter and rises to about one foot from the water surface from a 35 foot depth. The patch reefs are usually round with coral growth restricted to the outer rim and have a centrally depressed, coarse sand-filled area several feet lower than the coral rim. Sand mounds probably formed by worms are abundant on the surface of the central depressions. Massive corals are dominant on most patch reefs. Isolated groupings of coral heads are scattered on the lagoon floor (Figure 18).

Lagoonal sediments are quite variable with a silt sized calcium carbonate flour containing aragonite needles in some of the deeper areas, and coarser bioclastic sand adjacent to islands and reefs.

Alacran Reef contains five islands: Perez, Desertora, Desterrada, Pajaros, and Chica. These are sand cays without exposures of lithified rock of any type. The islands are low-lying and their outlines seem to vary seasonally with storms and changing wind direc-

FIG. 17. Profile of the end of a circular patch reef in lagoon north of Isla Perez.

tions. All cays support abundant vegetation and are nesting grounds for many species of birds, including the Sooty Tern (*Sterna fuscata*), Frigate bird (*Fregata magnificens*), Brown Noddy Tern (*Anoüs stolidus*), Royal Tern (*Thalasseus maximus*), Laughing Gull (*Larus atricilla*), Blue Faced Booby (*Sula dactylatra*), Brown Booby (*Sula leucogaster*) (identifications by J. D. Powell). A small shallow pond on Pajaros is surrounded by mangroves. Ponds on the islands are depressions formed apparently by the building up of coral and shell ramparts or spits around their margins. Although they are probably of a temporary nature, some of the mollusks (*Batillaria minima* and several nerites) collected on Alacran Reef seemed restricted to these ponds. The larger islands of Perez, Desertora, and Desterrada are situated on the leeward shelf. The islands of Chica and Pajaros are located on the southern tip of the inner reef flat. A sand bar called Desaparecida Bar forms an island during the summer but is cut down by wave action and disappears below water during the northerly winter winds. The beaches around the islands consist of a hash of mollusk shells and coral fragments. Low beach ridges of shell or fragments of staghorn coral are common (Figures 19 and 20).

FIG. 18. Large coral head of *Diploria* on lagoon floor near Isla Perez. Water depth is about five feet.

Alacran Reef as a whole is probably in an earlier phase of development than all the rest of the reefs of the Campeche Bank and the reefs of Vera Cruz and Anton Lizardo. This relative immaturity of Alacran Reef may be accounted for by its far greater size in relation with the other reefs, and it does not necessarily imply that it started later.

List of Species Identified

Collection of specimens from the Alacran Reef in July, 1959, was a joint effort by members of the expedition. Special credit is due Mr. Thomas Wright who curated the collection in the field. All corals listed were observed alive on the reef. Many of the Mollusca were not collected alive, but probably are living in the area. We are indebted to Dr. T. E. Pulley and Mrs. Winnie H. Rice for identifying the Mollusca. Dr. Federico Bonet identified many of the stony corals in the field. The senior author keyed out the stony corals brought back from the reef and accepts full responsibility for any misidentifications. Dr. Donald F. Squires verified the presence on the reef of *Acropora palmata, Acropora cervicornis, Agaricia agaricites, Porites porites* var. *furcata, Diploria clivosa, Montastrea annularis, Favia fragum,* and *Millepora* from specimens or photographs he examined. Octacorals were identified by Dr. F. M. Bayer through the courtesy

FIG. 19. Windward lagoonal beach on southern part of the island of Perez. Inset is closeup of sediment which is composed principally of fragments of *Acropora cervicornis* about three inches in length.

of Dr. Fenner A. Chace, Jr., Smithsonian Institution, United States National Museum. Bryozoa were identified by Dr. Alan Cheetham, Louisiana State University. The specimens listed below are deposited with the invertebrate collection at the Institute of Marine Science. A duplicate set of the octocorals has been deposited with the Division of Marine Invertebrates, United States National Museum. Marine plants were identified by L. Huerta who has made collections from many Mexican reefs (1958) The Polychaeta were identified by E. Rioja (1958). The Echinodermata were identified by M. E. Caso.

COELENTERATA

Hydrozoa

Millepora alcicornis Linnaeus

Anthozoa

Zoantharia

Acropora palmata (Lamarck)
Acropora cervicornis Lamarck
Agaricia agaricites (Linnaeus) (varieties not differentiated)

FIG. 20. Lee beach on southern part of the island of Perez where sediments consist principally of a hash of mollusk shells. Insert in lower part of photograph shows the inhabited part of Perez. The buildings face the lagoon.

Siderastrea radians (Pallas)
Siderastrea siderea (Ellis and Solander)
Porites astreoides Lamarck
Porites porites var. clavaria Lamarck
Porites porites var. furcata Lamarck
Favia fragum (Esper)
Diploria clivosa (Ellis and Solander)
Diploria strigosa (Dana)
Diploria labyrinthiformis (Linnaeus)
Colpophyllia amaranthus (Muller)
Manicina areolata (Linnaeus)
Montastrea cavernosa (Linnaeus)
Montastrea annularis (Ellis and Solander)
Mussa angulosa (Pallas) Oken
Eusmilia fastigiata (Pallas)

Octocorallia

(Identified by F. M. Bayer)

Briareum asbestinum (Pallas)
Plexaura homomalla (Esper)
Plexaura flexuosa Lamouroux
Eunicea tourneforti Milne Edwards and Haime
Eunicea calyculata (Ellis and Solander)
Plexaurella dichotoma (Esper)
Pseudoplexaura laevigata (Moser)
Pseudoplexaura porosa (Houttuyn)
Pseudopterogorgia americana (Gmelin)
Pterogorgia citrina (Esper)
Pterogorgia anceps (Pallas)
Gorgonia ventalina Linnaeus

POLYCHAETA

(Identified by E. Rioja)

Eurythoe complanata (Pallas)
Hesione picta Müller
Nereis riisei Grube
Eunice schemocephala Schmarda
Nematonereis hebes Verrill
Thelepus setosus (Quatrefages)
Branchiomma bairdi (M. Intosh)
Sabella melanostigma Smarda

Materials collected by F. Bonet *et al.*, in May 1955.
Additional material collected in 1959 is now in study.

BRYOZOA

(Identified by Alan Cheetham)

Cheilostomata

Rhynchozoon rostratum (Busk)
Ellisina latriostris (Osburn)
Hippopodina feegeensis (Busk)
Celleporaria magnifica (Osburn)
Styloma spongites (Pallas)
Tremogasterina mucronata (Smitt)
Celleporaria albirostris (Smitt)
Cleidochasma porcellana (Busk)
Parasmittina trispinosa (Johnston)
Escharoides costifera (Osburn)
Scrupocellaria maderensis Busk
Tetraplaria dichotoma (Osburn)

Cyclostomata

Lichenopora buski Harmer

MOLLUSCA

(Identified by T. E. Pulley and W. H. Rice)

Gastropoda

Emarginula phrixodes Dall
Diodora minuta Lamarck
Diodora listeri Orbigny
Lucapina suffusa Reeve
Lucapina philippiana Finlay
Hemitoma emarginata de Blainville
Acmaea jamaicensis Gmelin
Acmaea cf. *postulata pulcherrima* Guilding
Calliostoma zonamestum A. Adams
Calliostoma jujubinum Gmelin
Calliostoma sp.
Tegula fasciata Born
Cyclostrema cancellatus Marryat
Arene cruentata Muhlfeld
Turbo castaneus Gmelin
Caecum cf. *nebulosum*
Modulus modulus Linné
Batillaria minima Gmelin
Cerithium literatum Born
Cerithium variabile C. B. Adams
Cerithium sp.
Seila adamsi H. C. Lea
Alaba sp.
Triphora decorata C. B. Adams
Epitonium sp.
Melanella sp.
Cheilea equestris Linné
Hipponix antiquatus Linné
Strombus gigas Linné
Astraea longispina Lamarck
Astraea americana Gmelin
Astraea caelata Gmelin
Tricolia sp.
Nerita peloronta Linné
Nerita versicolor Gmelin
Nerita tessellata Gmelin
Neritina virginea Linné
Smaragdia viridis Linné
Littorina ziczac Gmelin
Nodilittorina tuberculata Menke
Rissoina (represented by three species)
Vermicularia knorri Deshayes
Caecum cf. *floridanum* Stimpson
Caecum cf. *cooperi* S. Smith
Strombus costatus Gmelin
Strombus raninus Gmelin
Trivia suffusa Gray
Cyphoma gibbosum Linné
Polinices lacteus Guilding
Sinum perspectivum Say
Natica canrena Linné
Cassis madagascariensis Lamarck
Cymatium martinianum Orbigny
Cymatium cynocephalum Lamarck
Tonna maculosa Dillwyn
Tonna galea Linné
Murex pomum Gmelin
Murex sp.

Drupa nodulosa C. B. Adams
Thais deltoidea Lamarck
Columbella mercatoria Linné
Anachis sp.
Nitidella nitidula Sowerby
Bailya intricata Dall
Busycon contrarium Conrad
Busycon spiratum Lamarck
Nassarius ambiguus Pulteney
Leucozonia nassa Gmelin
Fasciolaria tulipa Linné
Fasciolaria hunteria Perry
Pleuroploca gigantea Kiener

Ischnochiton sp.

Dentalium sp.

Arca zebra Swainson
Arca umbonata Lamarck
Barbatia cancellaria Lamarck
Barbatia domingensis Lamarck
Glycymeris pectinata Gmelin
Modiolus americanus Leach
Lithophaga nigra Orbigny
Isognomon alatus Gmelin
Pinctada radiata Leach
Pinna carnea Gmelin
Chlamys imbricata Gmelin
Lyropecten antillarum Recluz
Spondylus americanus Hermann
Lima scabra Born
Ostrea frons Linné
Xancus angulatus Solander
Olivella nivea Gmelin
Prunum labiatum Valenciennes
Hyalina avena Valenciennes
Conus spurius atlanticus Clench
Conus mus Hwass
Monilispira sp.
Bulla sp.
Atys caribaea Orbigny
Atys sandersoni Dall
Haminoea succinea Conrad
Odostomia sp.
Cavolina sp.

Amphineura

Scaphopoda

Pelecypoda

Lucina pensylvanica Linné
Codakia orbicularis Linné
Divaricella quadrisulata Orbigny
Chama macerophylla Gmelin
Trachycardium isocardia Linné
Trigoniocardia media Linné
Laevicardium laevigatum Linné
Antigona listeri Gray
Chione cancellata Linné
Petricola lapicida Gmelin
Tellina radiata Linné
Tellina interrupta Wood
Tellina candeana Orbigny
Arcopagia fausta Pulteney
Apolymetis intastriata Say

ECHINODERMATA
(Identified by M. E. Caso)

Brissus unicolor (Leske)
Eucidaris tribuloides (Lamarck)
Ophiothrix suensonii Lütken
Holothuria mexicana Ludwig
Euapta lappa (J. Müller)

MARINE PLANTS
(Identified by L. Huerta)

Algae

Ulva fasciata Delile
Enteromorpha lingulata J. Agardh
Valonia ventricosa J. Agardh
V. ocellata Howe
Dictyosphaeria favulosa (J. Agardh) Decaisne
Halimeda opuntia f. triloba Barton
H. tridens Lamouroux
Dictyota linearis Greville
Sargassum vulgare var. foliosissimum J. Agardh
Sargassum fluitans Boergesen
Turbinaria tricostata Barton
Liagora farinosa Lamouroux
L. pinnata Harvey
Amphiroa fragilissima Lamouroux
Hypnea cervicornis J. Agardh
Acanthophora spicifera Boergesen
Laurencia papilosa Greville

Spermatophyta

Diplanthera wrightii (Ascherson) Ascherson
Thalassia testudinum Koenig and Sims

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A Study of the Effects of Anesthetics on the Behavior and Physiology of Fishes[1]

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Abstract

The anesthetic effects of 21 chemicals were tested on the teleosts, *Fundulus parvipinnis*, *Girella nigricans*, and *Paralabrax clathratus*. Fifteen of the chemicals tested (ethyl alcohol, tertiary butyl alcohol, methylparafynol, chloral hydrate, chlorobutanol, tribromoethanol, sodium amytal, barbital, phenobarbital, tricaine methanesulfonate, urethane, meprobamate, chlorpromazine, and magnesium sulphate) induced similar behavioral patterns in the species tested, while six (morphine sulfate, reserpine, azacyclonal, iodoacetate, sodium cyanide, and sodium bromide) had no visible effects or were toxic. In the behavioral pattern were observed four major stages: (1) sedation; (2) loss of equilibrium; (3) loss of reflex reactivity; and (4) medullary collapse. The anesthetic sequence observed for fishes is similar to that described for higher vertebrates.

Functions such as opercular rate, pectoral fin rate, cardiac rate, and metabolic rate were related to the various stages of anesthesia. It is suggested that measurements of metabolism of fishes in mild anesthesia (sedation) are reliable estimates of basal metabolic rates. The metabolic costs of maintaining equilibrium and integration of the organ systems in *Fundulus* are discussed.

It is shown that a given depth of anesthesia can be maintained in a fish for periods from 12 to 24 hours and often to 48 hours by carefully controlling the concentration of anesthetic dissolved in the medium. Variables, such as temperature, acidity, ionic constitution of the medium, and the size of fish affect the rate of induction and the depth of anesthesia.

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[1] From a doctoral dissertation submitted to the University of California, Los Angeles, prepared under the supervision of Dr. Boyd W. Walker and Dr. Frederick Crescitelli of the Department of Zoology.

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Introduction

Anesthesia[2] is a physiologic state of protoplasm that is produced by many diverse agents and is characterized by a reversible insensitiveness of the cell, tissue, or organism. Although knowledge of anesthesia in higher vertebrates is extensive, little is known about the process in fishes. Several questions concerning fish anesthesia seem pertinent to understanding the phenomenon itself as well as a necessary background for progress in the fields of comparative physiology, pharmacology, and applied biology where anesthetics have been used as part of fishery technique. What anesthetics and what concentrations are effective in producing anesthesia in fishes? Is anesthesia a common phenomenon in fishes? Are the same states produced by different compounds? Is anesthesia in fishes similar to anesthesia in other vertebrates? What is the mode of action of anesthetics in fishes?

To answer these questions, two major experimental procedures were utilized during the study. In one procedure, fishes were exposed to various concentrations of anesthetics and the changes in behavior recorded as a function of time. In the other procedure the depth of anesthesia was related to changes in physiologic functions, such as heart rate and metabolic rate. Data on the use of anesthetics with fishes in applied biology are reported elsewhere (McFarland, 1959 and 1960).

ACKNOWLEDGMENTS

The author would like to thank Dr. Boyd Walker of the University of California, Los Angeles, for initiating his interest in anesthesia of fishes and for his many suggestions and guidance throughout most phases of the work. Drs. Frederick Crescitelli, Dermot B. Taylor, Blaine Levedahl, and Donald Cram all of UCLA and Dr. Carl L. Hubbs of Scripps Institution of Oceanography also gave advice and reviewed the dissertation.

Most of this research was accomplished at Marineland of the Pacific. To Dr. Kenneth

[2] The terms 'anesthesia' and 'narcosis' are considered synonymous for the purposes of this paper, although preference is given to anesthesia. Varied uses of the terms by different workers are discussed by Heilbrunn (1952, p. 582).

S. Norris, Curator, go the author's deepest thanks for willing assistance throughout the study. Messrs. John Prescott, Frank Brocato, Frank Calandrino, Phillip Schuyler, and Fred Lowe of Marineland, and Drs. Richard Rosenblatt, Jay C. Quast, and Mr. Hisao Arai of the University of California at Los Angeles assisted in many ways.

Dr. Frederick Munz kindly aided in measurements of cardiac rates, Dr. George Barlow made available a Warburg respirometer for determination of metabolic rates, and Mr. Aaron Klain and Mr. Wayne Baldwin of the University of California, Los Angeles aided in construction of equipment.

Materials and Methods

Capture and Care of Fishes

Specimens of the killifish, *Fundulus parvipinnis* Girard, were captured with a beach seine in south San Diego Bay, California. Opal eye, *Girella nigricans* (Ayres) were collected with beach seines, by pool bailing, and with tertiary amyl alcohol from tidepools at Palos Verdes, California. Specimens of the kelp bass, *Paralabrax clathratus* (Girard), were captured with fish traps at Santa Catalina Island, California. All specimens were returned to the laboratory at Marineland of the Pacific, Portuguese Bend, California and placed in continuously flowing copper treated sea water (0.1 ppm Cu^{++}) for a period of two weeks. This water was obtained from a large reservoir in which a wide variety of marine fishes have been maintained for several years without noticeable mortality. All experiments were performed at temperatures that varied between 18–21°C and 27°C. One group of *Fundulus* was adapted to fresh water for experiments with sodium amytal while a few pilot experiments were performed in fresh water with mosquito fish, *Gambusia affinis*. Otherwise all experiments were performed in sea water.

Fish were fed chopped shrimp and mackerel four times a week, but were not fed for 24 hours prior to an experiment. All fish thrived in captivity with the exception of a portion of the groups of *Fundulus* which appeared to suffer from malnutrition. Mortality was from 15–20 per cent in these groups and was not alleviated by excess feeding. Fish in a poor nutritional state were not used in experiments.

Experiments on Fish Behavior, Dosage, Period of Exposure, and the Depth of Anesthesia

Groups of four fish in one gallon jars were exposed to increasing concentrations of anesthetic. Temperature, light, and group isolation were controlled by immersing the jars in a water bath in partitioned compartments which were uniformly lighted. Anesthetics, after being dissolved, were allowed to stabilize for one-half to one hour before introduction of the experimental fish. *Fundulus* and *Girella* were used as experimental animals for most of the anesthetics tested. The fishes used were between 45–68 mm standard length.

Observations of each group of four fish under a particular treatment were made at 2, 5, 10, 15, 20, 30, 40, 50, 60 minutes and thereafter every half-hour until four hours had elapsed. A final observation was made at 12 hours. During each observational period external stimuli were imposed and the behavioral reactions of controls and anesthetized fish recorded. Visual stimulation was produced by casting a shadow over the jars, and vibrational stimuli were provided by tapping the rim of the jar. Observations of activity,

appearance, and equilibrium were recorded. Changes in observable rate functions, such as opercular rate and pectoral fin beats, were not recorded during dosage experiments since it was not usually possible to maintain a continuous record of each fish. Further, the curvature of the experimental tank and the positions of the fishes often made counting difficult.

Experiments Relating Physiologic Functions to the Depth of Anesthesia

Opercular and Pectoral Fin Rates. Discrete experiments were performed on both *Fundulus* and *Girella* with methylparafynol to relate opercular and pectoral fin rates to the depth of anesthesia. Individual fish were placed in one-liter beakers in a compartmented rack and the entire assembly immersed in a large aquarium with the beaker mouths above the surface. Aeration and overhead illumination were provided, and viewing ports were placed opposite each beaker in the aquarium wall.

Individual fish were placed in 500 ml of sea water identical with that for acclimation. This water also supplied the large aquarium and served as a temperature control (20 ± 1°C during experiments).

Opercular and pectoral fin movements were counted with a stop-watch. The time required for 10 cycles was recorded and converted into cycles per minute. The level of anesthesia was determined independently and based on criteria defined in paragraphs which follow. Throughout the experiments only half of the fish were anesthetized and water was changed in the beakers every hour during the recording periods. When individual fish were in deep anesthesia, the treated water was replaced with fresh water, recovery was followed, and the rates counted until the fish appeared normal. Rates were again determined at 24 hours, the experiment concluded, and the standard length and weight of each fish measured.

Cardiac Rate. Cardiac rates were determined during anesthesia with a four pen electroencephalograph. *Paralabrax clathratus* weighing 200 to 225 grams were used. Electrodes were made by straightening number six steel fish hooks. Leads were soldered to the eye of the hooks and insulated with polystyrene cement. Two electrodes were inserted into each fish. One electrode was inserted approximately one inch into the dorsal muscle mass directly behind the cranium while the other electrode was inserted ventral to the heart just beneath the skin of the isthmus.

The concentration of methylparafynol, the anesthetic, was changed during the course of each experiment to cause first intermediate narcosis, then deep narcosis, and finally death. Opercular and cardiac rates were recorded simultaneously on the tracing.

Metabolic Rate. Oxygen consumption of *Fundulus* was measured using the Warburg method (Umbreit *et al.*, 1957) to determine the possible metabolic effect of anesthetics. Fish weighing four to eight grams were placed in special Warburg flasks, of approximately 250 ml capacity, and the rate of oxygen consumption determined over a 24 hour period. Measurements were usually made every hour, except where metabolism was rapid enough to permit one-half hour recordings. The metabolic effects of four anesthetics, teriary amyl alcohol, methylparafynol, tricaine methanesulfonate, and chlorobutanol were examined at concentrations found capable of inducing sedation. Fish being tested were compared with untreated controls.

Fish were treated with anesthetic for three hours before each experiment. One hundred ml of sea water were used in each test and control flask.

To eliminate disturbance as much as possible, the entire unit was covered with a black cloth. At 20–24 hours the cloth was removed, and the overhead lights were flashed on and off 10 times every 10 minutes. This procedure was designed to disturb the fish and increase their metabolism.

Behavioral Changes in Fishes During Anesthesia and a Classification of Recognizable Stages

The use of several drugs on fishes has revealed a tendency for anesthesia to follow a similar and specific course for the species of *Fundulus*, *Girella*, and *Paralabrax* tested. This similarity has allowed several chronological levels or stages of anesthesia to be defined and classified. The compounds tested during the study are arranged in groups related either by common chemical structure or biological action (Table 1). Of the 21 compounds tested nine have high narcotic potency, three have medium potency, three have slight potency, while eight either have no anesthetic action or visible effect, or are acutely toxic. Of the 15 compounds having an anesthetic action, only chlorpromazine was acutely toxic at a low concentration. With the exception of meprobamate, only compounds with a narcotic potency of two or three (Table 1) are discussed in this paper.

Observation of behavioral changes in *Fundulus*, *Girella*, and *Paralabrax* indicates that four major anesthetic stages are involved in fishes; each stage constitutes a major deviation from normal behavior. Within each stage minor deviations can be detected, but only in Stages I and II are minor deviations acute enough to warrant classification. Minor deviations are designated as *planes of anesthesia* in accordance with medical terminology (Goodman and Gilman, 1955, chap. 3). Major characteristics of the *stages* and *planes of anesthesia* as defined from observation of *Girella* and *Fundulus* are summarized in Table 2. A more detailed diagnosis of the behavioral sequences follows.

Anesthetic Stages

Stage 0. Stage 0 is defined by normal behavior in the absence of anesthetics. Normal behavior can vary from high to low activity. However, fishes when placed in experimental jars show characteristic behavior which is definable, even when there is wide variation in activity. Under such conditions normal fish show marked reactions to the motion of objects outside the tank. In *Girella* the reaction begins with a forward and lateral movement, followed by a descent to the bottom with an increase in the movements of the pectoral and caudal fins. In discussions that follow this response is termed "fright" response without any anthropomorphic implication. The dorsal fin is erected during the fright reactions. A similar response is evident in *Fundulus*, but initial forward or lateral movements are somewhat restricted or absent, and the fish descends almost immediately to the bottom. The dorsal fin is erect and sculling movements of the pectoral fins are rapid in both species during stimulation.

Vibrational stimuli elicit a marked fright reaction in both *Girella* and *Fundulus* and are characterized by initial long darting movements followed by numerous shorter movements and descent to the bottom of the vessel.

Normal fish maintain position through pectoral fin movements. Undisturbed *Girella*

TABLE 1

Compounds tested to ascertain their properties in producing anesthesia of fish
The following symbols denote the relative anesthetic potency: 0, no effect; 1, slightly potent; 2, moderate potency; 3, highly potent; and T, toxic.

Compound used	Species	Mode of administration	Narcotic potency
Hydrocarbons			
I-Alcohols			
(1) Ethyl alcohol	*Fundulus parvipinnis*	Salt water	2
(2) Tertiary butyl alcohol	*F. parvipinnis*	Salt water	2
(3) Tertiary amyl alcohol	*Girella nigricans*	Salt water	3
	F. parvipinnis	Salt water	3
(4) Methylparafynol	*G. nigricans*	Salt water	3
	F. parvipinnis	Salt water	3
II-Halogenated alcohols			
(1) Chloral hydrate	*G. nigricans*	Salt water	2
	F. parvipinnis	Salt water	2
(2) Chlorobutanol	*G. nigricans*	Salt water	3
	F. parvipinnis	Salt water	3
(3) Tribromoethanol (Avertin)	*F. parvipinnis*	Salt water	3
Barbiturates			
(1) Sodium amytal	*F. parvipinnis*	Salt water	3
	F. parvipinnis	Fresh water	3
	F. parvipinnis	Soft water (chelated)	3
	F. parvipinnis	Distilled water (fortified)	3
	Gambusia affinis	Fresh water	3
(2) Barbital	*G. nigricans*	Salt water	1
(3) Phenobarbital	*G. nigricans*	Salt water	1
Inorganic salts			
(1) Magnesium sulphate	*F. parvipinnis*	Salt water	0
	F. parvipinnis	Fresh water	0
	Paralabrax clathratus	Intramuscular injection	3 T
(2) Sodium bromide	*F. parvipinnis*	Salt water	0
	F. parvipinnis	Fresh water	0
(3) Sodium cyanide	*F. parvipinnis*	Salt water	0 T
Tranquilizers			
(1) Reserpine	*F. parvipinnis*	Salt water	0
	P. clathratus	Intramuscular injection	0
(2) Meprobamate	*F. parvipinnis*	Salt water	3
	F. parvipinnis	Fresh water	3
(3) Chlorpromazine	*F. parvipinnis*	Salt water	1 T
	F. parvipinnis	Fresh water	1 T
(4) Azacyclonal	*F. parvipinnis*	Salt water	0 T
	F. parvipinnis	Fresh water	0 T
Miscellaneous compounds			
(1) M.S. 222 (Tricaine methanesulfonate) *	*G. nigricans*	Salt water	3
	F. parvipinnis	Salt water	3
(2) Morphine sulphate	*G. affinis*	Fresh water	0
(3) Diethyl carbamate (Urethane)	*G. nigricans*	Salt water	3
	F. parvipinnis	Salt water	3
(4) Iodoacetate	*F. parvipinnis*	Salt water	0 T

* Tricaine methanesulfonate will be referred to as M.S. 222.

and *Fundulus* hover a few inches over the bottom, but individual fish occasionally move to the top or bottom of the tank. In hovering, the body is maintained in a horizontal position, the opercular rate is relatively constant, and pectoral fin movements compensate for thrust created by the respiratory currents. When undisturbed, the color of *Girella* is usually olivaceous while *Fundulus* is normally whitish accented with grayish-black vertical bars. Disturbance causes a slight darkening in *Girella*. However, no change in color was detected in *Fundulus* when disturbed.

TABLE 2

Synopsis of the major stages and planes of anesthesia for fishes
Stages are based on observation of the induction of anesthesia for
Girella nigricans and *Fundulus parvipinnis*

Anesthetic stage	Observed change in Behavior			
	Reaction to visual stimuli	Reaction vibrational stimuli	Equilibrium (Eq.) and muscle tone (M.T.)	Respiratory rate
Stage 0	Reactive	Reactive	Normal	Normal
Stage I				
Plane 1	Slightly reactive	Reactive	Normal	Normal
Plane 2	No reaction	Slight to no reaction	Normal	Normal
Stage II				
Plane 1	No reaction	Slight to no reaction	Partial loss Eq.	Increase
Plane 2	No reaction	Slight to no reaction	Complete loss Eq. & M.T.	Rapid decline
Stage III	No reaction	No reaction	Complete loss Eq. & M.T.	Slow, decrease in amplitude of opercular movements
Stage IV	No reaction	No reaction	Complete loss Eq. & M.T.	Ceases

Stage I. This stage is defined as a partial or total lack of reaction to external stimuli. The color may change but only to a moderate degree. Equilibrium is normal. Stage I can be separated into two planes as follows:

Plane 1 is indicated by a reduction in the fright response to visual stimuli. Both species move more slowly when stimulated and sink to the bottom very slowly. The dorsal fin is rapidly erected, but pectoral fin movements are not increased as much as in normal fish. Both species react to vibrations by marked fright reactions in a manner identical with controls (Stage 0).

Equilibrium is maintained in both species. In general they show less activity than controls and tend to hover quietly over the bottom. A slight dispersion of melanin usually occurs in *Girella*, imparting a grayish cast to the fish. Color change is most often not noticeable in *Fundulus*. Opercular rate and pectoral fin rate in undisturbed fish are normal or only slightly lower than controls.

Plane 2 is characterized by a lack of reaction in response to external stimuli. The fish hover over the bottom and show no fright reaction to visual stimuli. Fright reaction to vibration is modified in both species. Early in Stage I, plane 2 vibrational stimuli elicit rapid darting movements. These responses are not followed by the sequence of events seen in controls or in Stage I, plane 1 (descent, increased fin rates). Instead, the fish stop and return to a hovering position after the initial darting movement. The dorsal fin is not erected in *Girella* or *Fundulus*. Late in Stage I, plane 2 vibrational stimuli elicit only a barely perceptible response.

Equilibrium during both planes of Stage I is not disturbed. The opercular rate is normal or slightly lower than in controls, and the pectoral and caudal fin movements are compensatory to the respiratory currents. The fish show no signs of distress unless anesthetic concentrations are high. The earliest evidence of loss of equilibrium accompanies transition from Stage I to Stage II.

Stage II. This stage differs from Stage I by a partial to total loss of equilibrium. The lack of reaction to visual stimuli exhibited by fishes in Stage I is maintained. Color be-

comes darker. Opercular rate is not normal and a variable loss in the synchrony of fin movements is noted. A partial to total loss of muscle tone occurs. This stage can be separated into two planes as follows:

Plane 1 differs from Stage I, plane 2 by the appearance of distress and imbalance in equilibrium. In undisturbed *Girella* there is first an increase in random movements as compared to the quiet hovering characteristic of Stage I, plane 2. This is followed by active swimming, rolling movements, and a tendency for individual fish to lie temporarily on their sides. Stage II, plane 1 is first indicated in *Fundulus* by a tilting of the body axis from the normal horizontal position until the snout touches the bottom. The tilt is slight at first (about 30° angle) but increases slowly until the fish is standing on its snout perpendicular to the bottom. Individuals of *Fundulus* then roll slightly and tend to lie on their sides.

Swimming in both species is uncoordinated and induced primarily by caudal fin and body movements. Beating of the pectoral fins is continued, but their function with reference to balance and position is disturbed. Both species darken, and both increase the opercular rate as discussed in the section on rates. The fish fail to respond to external stimuli, except for occasional darts following vibrational stimuli. Even these responses are limited and cease almost immediately after cessation of the stimuli. Individual fish swim upside down in late Stage II, plane 1.

In plane 2 there is complete loss of equilibrium and cessation of swimming movements. Both species lie upside down on the bottom of the tank. Fin movements are markedly uncoordinated or absent. The muscles are flaccid and fish lifted from the water are limp and do not react unless pinched. The opercular rate declines rapidly but the amplitude of each stroke is unmodified. In *Girella* the body color becomes quite dark, while in *Fundulus* it may or may not darken.

Stage III. This stage is defined by a severe upset in respiratory rate. The rate declines rapidly from the low rate of Stage II, plane 2, as discussed in a following section. The amplitude of each opercular beat becomes large and exaggerated. Each fish completely loses its equilibrium, movement, and muscle tone, as in Stage II, plane 2, and fails to react to strong external stimuli. Both species become very dark.

Stage IV. Stage IV is defined by respiratory and cardiac collapse. The respiratory movements cease, the opercles are spread and the pectoral fins usually are in an extended position perpendicular to the body. Each specimen lies upside down on the bottom, although an occasional individual is buoyant and floats at the surface. Death is assumed to have occurred when opercular movements have ceased for approximately one minute. Slow cardiac contractions continue for several minutes after cessation of opercular movements. No recovery is possible if the fish is left in the anesthetic solution. However, if the fish is removed, the condition can be reversed and the fish can return to normal.

Deviations from the Behavioral Pattern

With ethyl alcohol individual fish showed an extreme nervousness manifested by heightened swimming activity prior to onset of Stage I. This tendency did not abate until the induction of Stage I-2, but a delayed response to vibrational stimuli was often noted in this stage. The distress was no longer evident after the onset of Stage II; the pattern of anesthesia was normal. However, several deaths occurred at 137 and 183 mM/l, although the average depth of anesthesia induced did not exceed that of Stage II-1.

One adverse side effect was noted with the use of urethane. A temporary distress was noted in *Fundulus* exposed to 10 mM l and above. It was evident as a continued swimming against the side of the tank. This is similar to behavior induced in *Fundulus* by chlorpromazine (McFarland, 1959) and to the behavioral change reported by Keller and Umbreit (1956) in *Lebistes reticulatus* with LSD (lysergic acid diethylamide). The fish were nonreactive to visual stimuli during this period.

Tribromoethanol, chlorobutanol, and M.S. 222 (Tricaine methanesulfonate) cause a very noticeable loss of reactivity in Stage I-2. Groups in this stage at the conclusion of the experiments did not react to strong vibrational stimuli. Such stimuli (striking the jar on a table) usually elicited darting movements from fishes in Stage I-2 when narcotized with other anesthetics. It is possible that the intensity of anesthesia at any given stage induced with tribromoethanol, chlorobutanol, and M.S. 222 is related to the high anesthetic potencies and molecular weights of these drugs in comparison with most of the other anesthetics used (Tables 3 and 4).

TABLE 3

Synopsis of the dosage-response results obtained for *Fundulus parvipinnis*

Effective concentrations for inducing various levels of anesthesia are given in mM/l (millimoles per liter).

Anesthetic	Molecular weight*	Narcotic potency	Minimal dose (M.D.)	Fatal dose (F.D.)	F.D./M.D.
Ethyl alcohol	46	0.2	92.00	228	2.5
Tertiary butyl alcohol	74	1.0	21.00	112	5.3
Urethane	89	1.4	2.00	.....	22.0†
Chloral hydrate	165	2.5	2.60	21	8.1
Tertiary amyl alcohol	88	3.2	1.00	12	12.0
Methylparafynol	98	4.1	1.20	9.5	7.9
Sodium amytal‡	248	76.5	0.07	.....	.....
Chlorobutanol	177	82.0	0.05	0.77	15.4
Sodium amytal§	248	190.0	0.04	0.35	10.0
M.S. 222¶	261	147.0	0.03	0.24	7.1
Tribromoethanol	283	267.0	0.01	0.47	47.0

* Molecular weight rounded to nearest whole number.
† Based upon an estimated fatal dose.
‡ *Fundulus* adapted to salt water.
§ *Fundulus* adapted to fresh water.
¶ See Table 1.

TABLE 4

Synopsis of the dosage-response results obtained for *Girella nigricans*

Effective concentrations for inducing various levels of anesthesia are given in mM/l.

Anesthetic	Molecular weight*	Narcotic potency	Minimal dose (M.D.)	Fatal dose (F.D.)	F.D./M.D.
Urethane	89	1.0	3.84	38.40	10.0
Chloral hydrate†	165	4.5	1.10	16.00	14.5
Tertiary amyl alcohol	88	2.6	1.70	12.00	7.1
Methylparafynol	98	5.5	1.20	8.20	6.8
Chlorobutanol	177	64.0	0.05	0.75	15.0
M. S. 222§	261	192.0	0.03	0.20‡	.....

* Molecular weight rounded to nearest whole number.
† Experiment terminated at three hours. Values given are estimates.
‡ Fatal dose estimated; probably higher.
§ See Table 1.

Similiaity Between the Stages of Anesthesia and Earlier Descriptions of Anesthesia in Fishes

The sequence of behavioral changes described from anesthetized *Fundulus* and *Girella* are remarkably similar to behavioral disturbances of other fishes described by earlier workers, and indicate that anesthesia is quite uniform in fishes. Several workers have described portions of the anesthetic pattern; most important descriptions are those of Adams, *et al.*, 1926; Baudin, 1932a; Broun, 1928; Lévy, 1928; Meunch, 1956, 1958; Scheiner, 1945; Vivien, 1941; and Witjens *et al.*, 1947.

The initial period of excitation, described by most workers when fishes are exposed to a drug, was produced in *Fundulus* and *Girella* only when the initial concentration of drug was high enough to rapidly induce a complete sequence of anesthetic stages. No excitation was noted at concentrations of drugs that induced only Stages I and II or that slowly induced complete anesthesia. Since early results are most often for concentrations that would be lethal, the excitation reported is considered a reaction to strong stimulation of peripheral receptors such as taste and common chemical sense. Furthermore, similar excitation is induced by acids and many other irritants that have no anesthetic action. Therefore, such excitation cannot be considered a reaction common to anesthesia in fishes.

The period of calm is equivalent to Stage I, while the repeatedly observed disturbance in equilibrium accompanied by uncoordinated swimming is equivalent to Stage II-1. The complete loss of equilibrium reported by other workers is equivalent to the onset of Stage II-2. However, the flaccidity of muscles, the decline in opercular rate, and the loss of reflex reactivity often noted are more difficult to equate with the anesthetic stages defined in this investigation because early descriptions of anesthesia lack precision and because variations occur between species.

Relationship Between Dosage and Anesthesia

Dosage and the Pattern of Anesthesia

Increased dosage of anesthetics decreased the time for induction of each stage and increased the resultant depth of anesthesia. Data on which these conclusions are based are presented graphically for tertiary amyl alcohol, chloral hydrate, and tribromoethanol in Figures 1a, 1b, 2 and 3. Similar figures for other anesthetics reveal the same tendency (McFarland, 1959).

At high concentrations an initial period of excitation was noted with all anesthetics. Also, compression in the pattern of anesthesia often eliminated Stage I. At low concentrations not sufficient to induce complete anesthesia rapidly, the normal sequence of stages was observed.

The Control of Anesthesia

Various depths of anesthesia were induced and maintained for long periods in both *Girella* and *Fundulus* by varying the concentration of anesthetic. In several experiments, groups were left exposed to anesthetic for 24 to 48 hours. Groups of *Girella* exposed to 1, 2, and 3 ml of tertiary amyl alcohol per gallon (2.4, 4.8, and 7.2 mM/l) were maintained for 48 hours (Figure 1a). At 24 hours the same stages persisted as

indicated for 12 hours. The groups at 2 and 3 ml/gal. were still in Stage I-2 at 48 hours while the group at 1 ml/gal. was in Stage I-1. Similar maintenance of anesthesia was obtained with groups of *Fundulus* exposed for 24 hours to tertiary amyl alcohol, methylparafynol, chlorobutanol, and tribromoethanol.

Results, therefore, indicate that all anesthetic stages from I-1 to III can be controlled and maintained for considerable periods of time by varying the concentration of anesthetic.

Examination of Figures 1a, 1b, 2, and 3, and results for the other anesthetics (Tables 3 and 4; compare minimal and fatal dosages) reveal that the tolerance of both *Fundulus* and *Girella* to dosage can be very narrow. This is particularly true when the dosages necessary to induce and maintain two adjacent anesthetic levels are compared. In general, depending on the anesthetic, the amount necessary to maintain Stage I-2 is 1.25 to 2.0 times that necessary to maintain Stage I-1 for 12 hours (McFarland, 1959). Doubling the dosage appears to increase the depth of anesthesia by one level (plane) at any stage.

Narcotic Potency in Different Species of Fish

The concentrations of the various anesthetics necessary to induce Stage II-1 during 12 hours can be used to compare the potencies of the various anesthetics. Values obtained for *Fundulus* and *Girella*, using urethane as a basis for comparison and assigning it a value of one, are given in Tables 3 and 4. Tribromoethanol was the most potent, while M.S. 222, sodium amytal, and chlorobutanol had slightly lower potencies. Chloral hydrate, tertiary amyl alcohol, and methylparafynol had moderate and similar potencies, whereas tertiary butyl alcohol and urethane had low potencies. Ethyl alcohol had very low potency. Each compound produced an equal depth of anesthesia at approximately the same concentration in both *Fundulus* and *Girella*.

Comparison of dosages reported for other species of fishes by other workers support this conclusion. For instance, using ethyl alcohol, Fühner (1912) reported that concentrations between 304 and 325 mM/l induced complete loss of reflex reactivity (Stage III) in *Carassius auratus*, and the fish died after several hours exposure. In this investigation, ethyl alcohol at concentrations between 250 to 350 mM/l induced Stage III in *Fundulus* and also was ultimately fatal. Using M.S. 222, Pickford (1953) reported a concentration of 0.13 mM/l induced complete anesthesia (Stage III) in *Fundulus heteroclitus*. This depth of anesthesia was also induced in *Girella* at 0.13 mM/l with M.S. 222, but a slightly higher concentration between 0.15 and 0.20 mM/l was required for *Fundulus parvipinnis*. The results of Unger (1918), Hara (1924), and Aitken (1936) for chloral hydrate; of Hara (1924) and Aitken (1936) for urethane; of Nelson (1953) and Webb (1958) for M.S. 222; and of Burrows (1952) and Nelson (1953) for chlorobutanol are also in accord with concentrations required to induce a given depth of anesthesia in *Fundulus* and *Girella*. In fact, this phenomenon of similar effects of similar dosages seems general, since anesthetics at approximately the same concentration have been shown to induce a given depth of anesthesia in a diversity of organisms (Winterstein, 1926).

It may be predicted that concentrations effective in inducing various depths of anesthesia in *Fundulus* and *Girella* can be expected to induce at least approximately the same depth of anesthesia in most species of fishes. Some variation is to be expected,

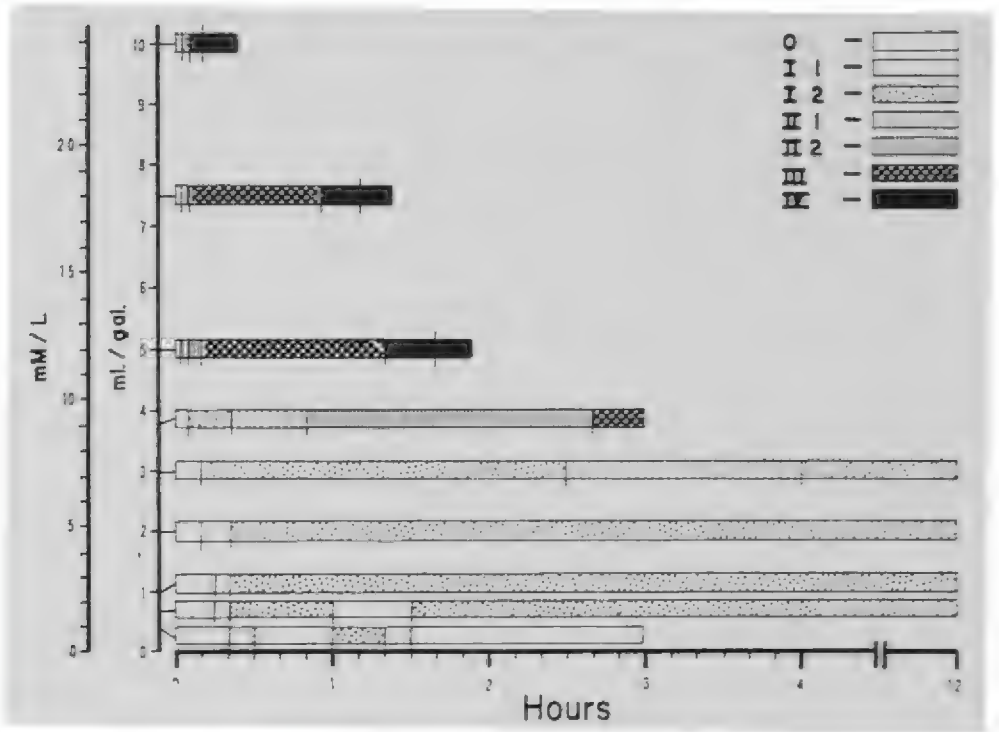

FIG. 1a. Tertiary amyl alcohol anesthesia of *Girella nigricans*. The abscissa represents time in hours: the ordinates represent anesthetic concentration in ml/gal. of sea water or in mM/l. Each horizontal bar expresses the dosage-time response of a group of four fish. The symbols refer to the stages and planes of anesthesia as defined in the text. The insert in the upper right corner relates the numerical equivalents of the various stages to the symbols of the figure. The small lines projecting downward from each bar are to assist in determining anesthetic level. The vertical line running through the black bars denotes the time of total mortality.

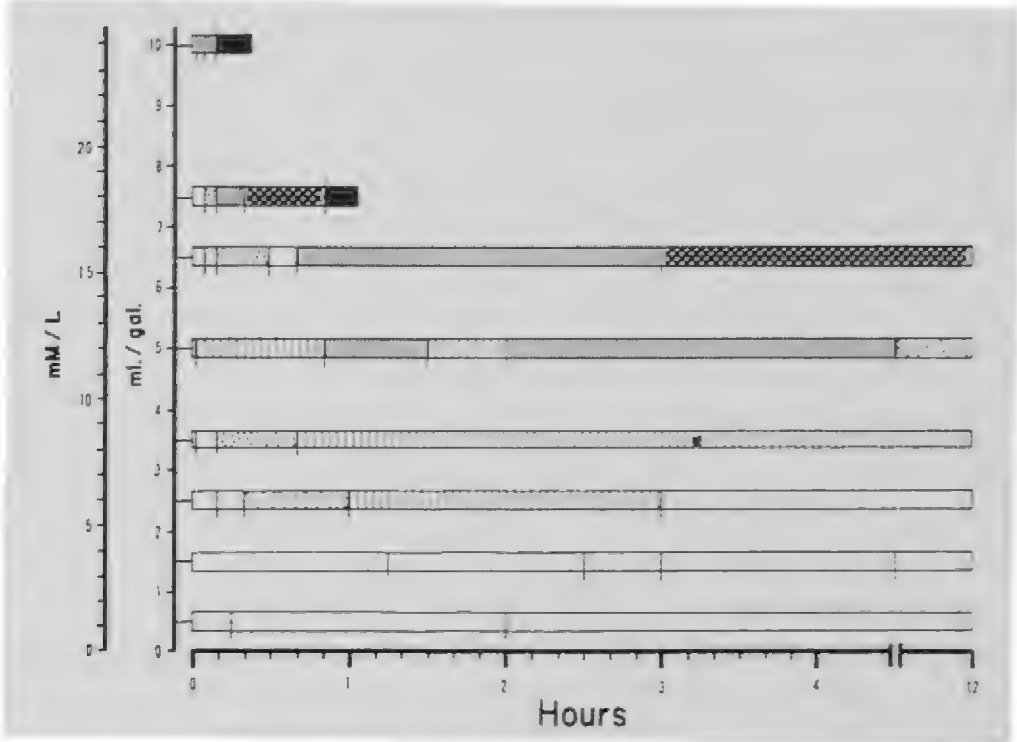

FIG. 1b. Tertiary amyl alcohol anesthesia of *Fundulus parvipinnis*. The abscissa, ordinates, and coding system are the same as for Figure 1a.

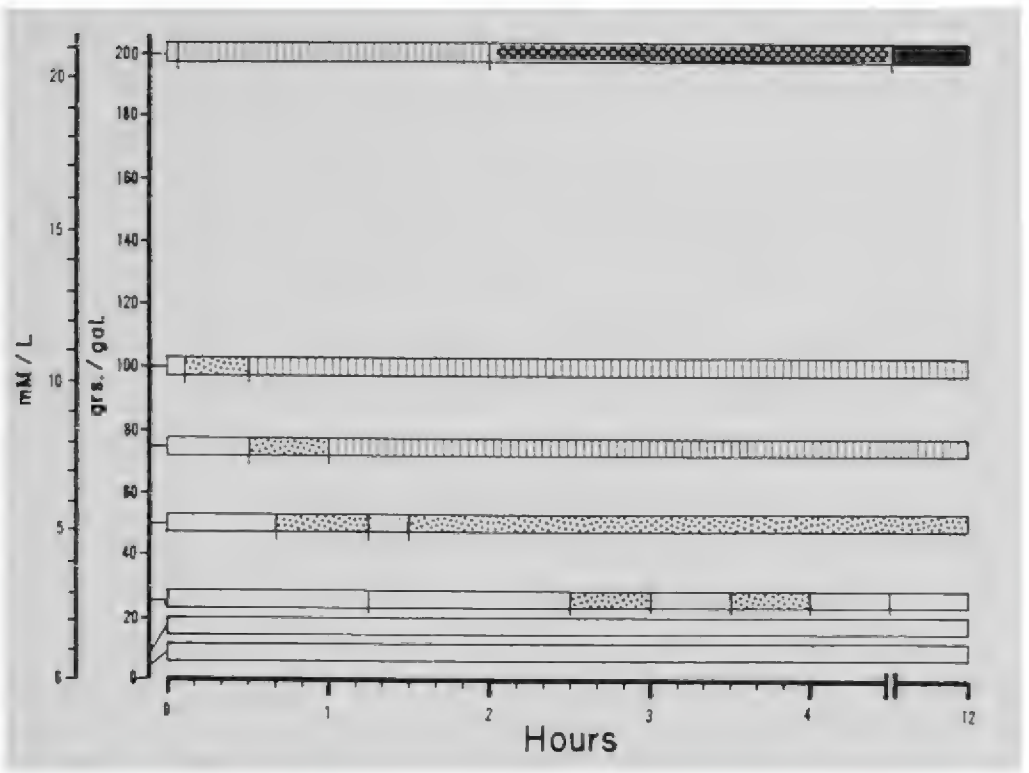

FIG. 2. Chloral hydrate anesthesia of *Fundulus parvipinnis*. The abscissa, ordinates, and coding system are the same as for Figure 1a.

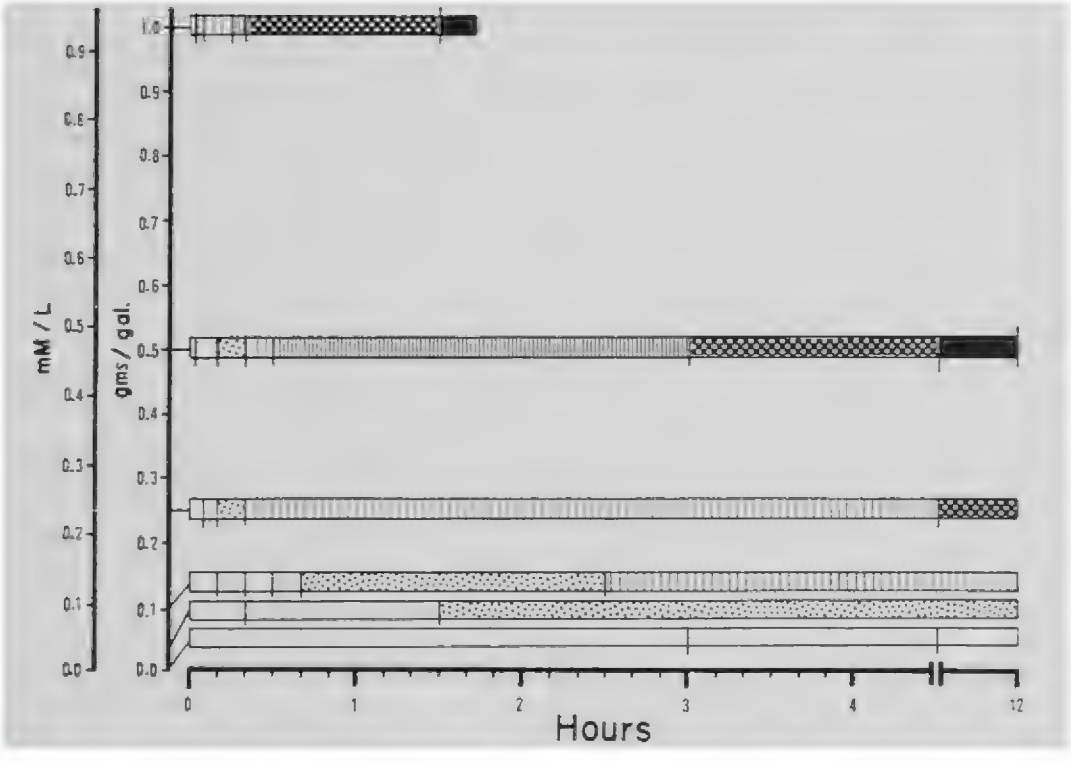

FIG. 3. Tribromoethanol (Avertin) anesthesia of *Fundulus parvipinnis*. The abscissa, ordinates, and coding system are the same as for Figure 1a.

particularly since temperature, size, acidity, and salt concentration of the medium have been shown to affect the rate and depth of anesthesia.

Molecular Weight and Narcotic Potency

Narcotic potency was found to be correlated with molecular weight (Tables 3 and 4). In addition, the minimal and fatal doses (Tables 3 and 4; considered as the concentration of anesthetic necessary to induce Stages I-1 and IV, during 12 hours, respectively) and dosages necessary to control State I-2 (reported elsewhere, McFarland, 1960) parallel the narcotic potencies. A smaller amount of anesthetic is required to induce equinarcotic levels as the molecular weight increases. Chloral hydrate was the only exception.

Fühner (1912), Tiffeneau and Dorlencourt (1923), Tiffeneau and Torres (1924) and Broun (1928), working with a variety of fishes and different compounds, all showed a positive correlation between narcotic potency and increasing molecular weight. More recently, Lindenberg and Gary-Bobo (1951) measured the activities (effective thermodynamic concentrations) of a series of homologous alcohols in the body fluids of the fresh water gudgeon, *Gobio fluviatilis*, and the marine blenny, *Blennius pholis*. Their studies also indicate a positive correlation between narcotic potency and increased molecular weight. In addition, they found that the activities of anesthetics of different molecular weight in the body fluids of both species were approximately the same at equal depths of anesthesia. Lindenberg's and Gary-Bobo's findings are in agreement with the theory proposed by Ferguson (1939 and 1951) that equal depths of narcosis are induced in organisms by different anesthetics when their activities attain the same level in the target organ. Unfortunately, similar data are not available from this investigation to determine whether the same condition prevailed in the tissues of *Fundulus* and *Girella*.

Molecular weight and the rate of anesthetic induction. The rate of induction of anesthesia is correlated with molecular weight. For instance, in *Fundulus* the induction of Stage I-2 was rapid (less than 15 minutes) with tertiary amyl alcohol, methylparafynol, and urethane. With chloral hydrate, chlorobutanol, and tribromoethanol the induction time was 40, 60, and 90 minutes respectively. It is possible that the lags in induction time for the latter anesthetics are related to their increased molecular size and a decreased rate of penetration of anesthetic through the gills and other membranes of *Fundulus*.

The time required for induction of anesthesia was always longer for *Fundulus* than for *Girella*, although, with the exception of tertiary amyl alcohol, equal depths of anesthesia were ultimately induced in both species at similar concentrations with all of the anesthetics used. For instance, in *Girella*, Stage I-2 was induced with chlorobutanol in 10 minutes rather than in 60 minutes as in *Fundulus*. There may be a marked difference between *Girella* and *Fundulus* in the permeability of the gills and other membranes. Superficial differences in anesthesia may often reflect differential permeabilities to penetration by anesthetics rather than different intracellular effects.

Major Factors Which Affect the Rate of Induction and the Depth of Anesthesia in Fishes

Several factors appear to cause changes in the rate of induction and the depth of anesthesia attained in fishes. The most important factors are the size of fish, the temperature, the acidity of the medium. and the chemical constitution of the medium. Each of these are considered separately.

Random Variation

Variations between similar sized fish were determined by observing the time of induction of various depths of anesthesia in similar-sized groups of *Fundulus*. using a constant concentration of methylparafynol (Figure 4). Variation within the group included two levels (planes). Stage III was induced in four out of five groups at 12 hours while one group was in Stage II-2. Variation in the depth of anesthesia of individual fishes was greater than for the groups. For instance. of 20 fish anesthetized (Figure 4), after 12 hours two fish were in Stage II-1, one fish in Stage II-2, 15 fish in Stage III. and two fish in Stage IV. The anesthetic stages represented by individuals spanned four levels, rather than two, as judged from Figure 4.

Size

Size, age. and metabolic rate (also a function of size) are some of several parameters that are known to influence the rates and depths of anesthesia in mammals (Goodman and Gilman. 1955. pp. 43–45). Little is known concerning the effect of size for fishes, but a few workers have reported that larger fish are more susceptible to anesthetics (Kochman. 1913; Keys and Wells. 1930; and Meunch. 1956). In contrast, Adams *et al.* (1926) and Witjens *et al.* (1947) ascertained no size effect on the induction times of anesthesia in specimens of *Carassius auratus* that varied between 2 to 10 grams. However, their experiments were of short term (less than 40 minutes) and were performed at concentrations that would have been lethal for longer periods. The experiments of Keys and Wells and of Meunch covered periods up to 24 hours and were performed at sub-lethal concentrations.

The effect of size on the rate and depth of anesthesia was examined for various sized groups of *Fundulus* and susceptibility was found to increase with size. Five groups of *Fundulus* were exposed to methylparafynol (Figure 5). There was a definite tendency of deeper stages of anesthesia to be induced in larger fish. Group A, containing the smallest fish. was the only group in which a stage higher than II-1 was not induced, while group E, containing the largest fish, was the only group in which Stage III was induced. Anesthesia in groups B. C. and D was relatively uniform. Several fish in groups B. C, and D actually entered Stage III (normal variation), but the numbers were not sufficient to cause a shift in the mean anesthetic value for the groups. These results support the suggestions of Kochman, of Keys and Wells. and of Meunch. Whether the increased susceptibility of larger fishes is the result of changes in surface-volume relations, differences in metabolic rate, or some other parameter related to size is unknown.

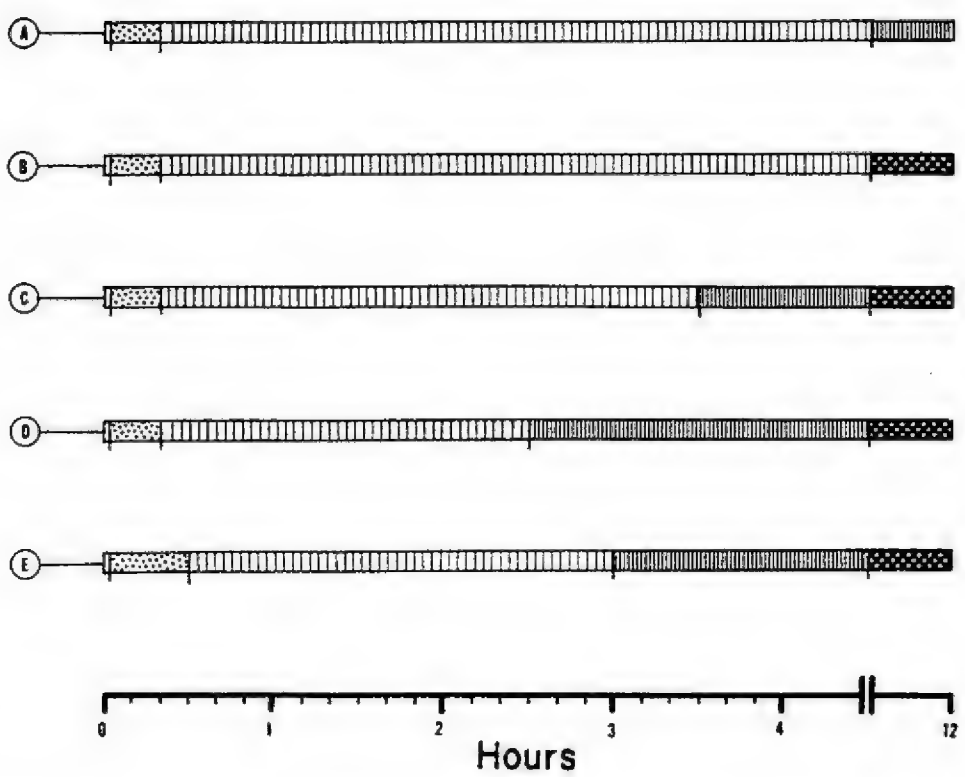

FIG. 4. Variation of anesthesia induced in similar sized groups of *Fundulus parvipinnis*. Methylparafynol, at a concentration of 3.0 ml/gal. (7.3 mM/l) of sea water, was used on each group as the anesthetic. Letters refer to individual groups, each of which contained four fish. The mean weight and range in grams of each group were: A, 6.58 (5.8–7.2); B, 6.0(5.6–6.5); C, 5.98(5.3–7.1); D, 6.7(5.5–7.6); and E, 6.7(5.2–8.0). The coding symbols refer to the various anesthetic stages as defined in the text and are the same as for Figure 1a.

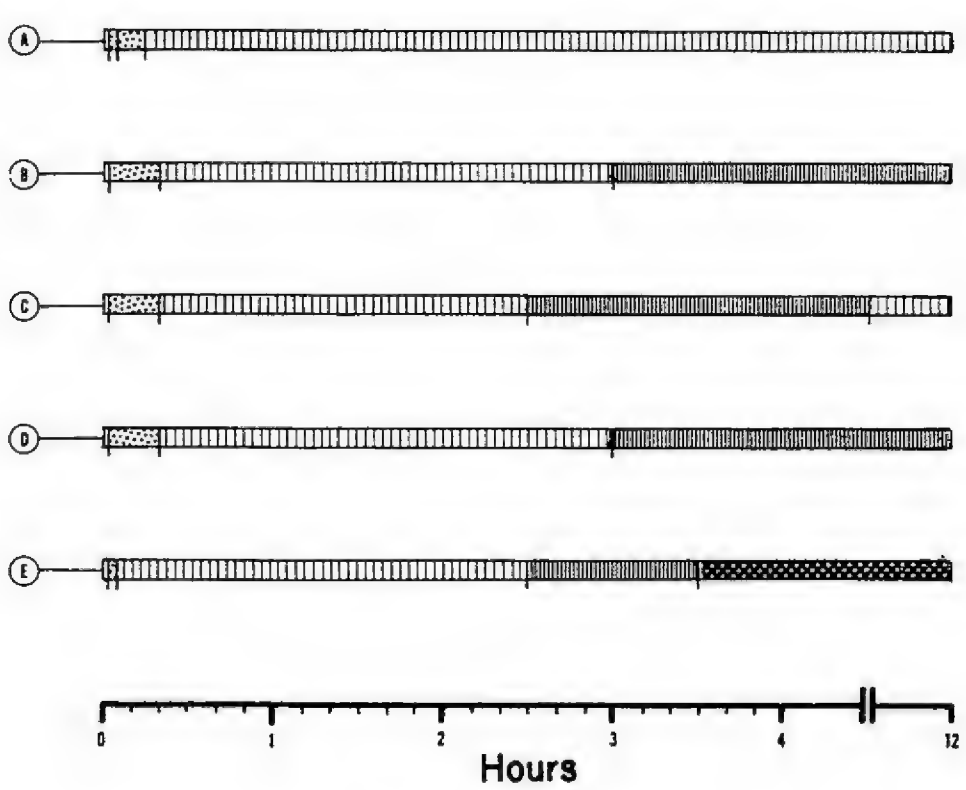

FIG. 5. Variation of anesthesia induced in different sized groups of *Fundulus parvipinnis*. Methylparafynol, at a concentration of 3.0 ml/gal. (7.3 mM/l) of sea water, was used as the anesthetic with each group. The letters refer to individual groups, each of which contained four fish. The mean weight and range in grams of each group were: A, 2.23(1.78–2.45); B, 3.71(3.25–4.25); C, 3.84(3.32–4.48); D, 4.89(3.90–5.58); and E, 7.93(6.67–9.86). The coding symbols refer to the various anesthetic stages defined in the text and are the same as for Figure 1a.

Temperature

The effects of temperature on the rate and the depth of anesthesia of *Fundulus* were studied using tertiary amyl alcohol and M.S. 222. Temperature acclimated groups of *Fundulus* were tested at each acclimation temperature, 27° ± 1°C and 12° ± 0.5°C.

Anesthesia with tertiary amyl alcohol was induced more rapidly and reached greater depth at higher temperatures. In addition, differences were more pronounced with high concentrations of the alcohol. The rate of anesthetic induction, judged by time of total mortality (Stage IV) and by the onset of Stage II–1 was from two to four times more rapid at 27°C than at 12°C.

As with tertiary amyl alcohol, induction times with M.S. 222 were faster at the higher temperature. In contrast, however, the depth of anesthesia induced at the higher temperature was not greater than at the lower temperature. There were many cases of reversal, the lower temperature producing deeper anesthesia. This reversal is related to the length of exposure of the fish to the anesthetic and consequent metabolic utilization of M.S. 222. In fact, metabolic evidence presented later indicates M.S. 222 is depleted more rapidly with time than other anesthetics. The readily ionizable groups of M.S. 222, in comparison to the simple, stable structure of tertiary amyl alcohol, may explain the temperature-reversal effects found.

Several workers have reported that the time between treatment and loss of reflex reactivity in fishes is dependent on temperature. A twofold decrease in the time for loss of reflex reactivity at the higher temperature is reported by Tiffeneau and Broun (1937) for *Gobio sp.* acclimated and tested 15°C and 25°C. Witjen *et al.* (1947) report similar changes for *Carassius auratus* acclimated and tested at 10° and 20°C. The results reported in this paper are in close agreement with the results of Tiffeneau and Broun and of Witjens and co-workers, but in contrast to the greater deviations reported by Regnier *et al.* (1938) and Unger (1918). These workers report loss of reflex reactivity to be from 4 to 10 times more rapid at the higher of two temperatures 15°C apart. However, in both these studies the fish were subjected to sudden temperature changes and were not acclimated to the test temperature.

The results suggest that at the higher temperature of acclimation the rate of induction of anesthesia is twice as fast for differences of 10°C. Interestingly, such changes in rate are characteristic of the ratio of velocity constants of most chemical systems (Q_{10} between 2 and 3, Glasstone, 1946; Clark, 1948). In his recent review, Bullock (1955) showed that metabolic compensation for temperature is common, although not universal, to poikilothermic organisms. Generally, this compensation is not complete, but is less than the metabolic responses of unacclimated animals (lower Q_{10}). The smaller effects obtained with acclimated fishes as opposed to unacclimated fishes may be explained by the more constant metabolic rates among acclimated fish. Therefore, temperature effects on anesthesia of fishes are the result of an interaction between metabolic changes of the organism and physical changes in the chemical activity of the anesthetic itself. Where fishes are exposed to changes in temperature during anesthesia, deviations in the rate of induction of anesthesia with a Q_{10} greater than two can be expected.

Acidity and Ionic Composition

Several workers have indicated changes in reaction time with changes in acidity. In their investigations Tiffeneau *et al.* (1933) and Tiffeneau and Broun (1935) found the

time for loss of reflex reactivity to be twice as fast in water acidified with lactic acid as in unacidified water and twice as long in water made alkaline with sodium hydroxide. These authors suggest that the differences are explainable by differences in permeability, caused by the acidity of the medium. In contrast to these findings, Lopez-Lomba (1922a-b), Regnier (1938), and Regnier *et al.* (1938) investigating the action of several alkaloids on *Gasterosteus aculeatus* found the time for loss of reflex reactivity to be increased by increased acidity.

It is probable that the pH of the medium not only affects the permeability of the gills to an anesthetic, as suggested by Tiffeneau *et al.* (1933) but also affects the chemical properties of the anesthetic and therefore the absorption rate. Chemical change is most probable among alkaloids and other molecules that readily hydrolize in alkaline solutions. Such chemical change will be less frequent among anesthetics used in a form other than the salt (Witjens *et al.*, 1947).

Recently, Onkst *et al.* (1957) have reported an antagonism of anesthesia produced in *Lebistes reticulatus* with sodium amytal in the presence of calcium. They report that calcium binding substances, such as citrate ion or disodium ethylenediamine tetraacetate (EDTA), are effective in combating this antagonism but they do not propose a locus of action.

Pilot experiments performed during this study on both *Girella* and *Gambusia affinis* indicated that barbiturates (sodium amytal, phenobarbital, and barbital) were of limited use for the induction of anesthesia, particularly in salt water (McFarland, 1954). Subsequent experiments with sodium amytal were designed to check the effects of the narcotics on *Fundulus* when adapted to marine and fresh water conditions (Table 3). In *Fundulus* adapted to salt water, all stages except IV were induced at 0.7 mM/l. In contrast, in *Fundulus* adapted to fresh water, all stages including IV were induced at 0.35 mM/l. Similar differences in the depth of anesthesia were obtained at lower concentrations, and again anesthesia was deeper in the groups adapted to fresh water.

The deeper and more rapid induction of anesthesia in *Fundulus* adapted to fresh water suggested that the salts in sea water may antagonize the action of sodium amytal. In view of the calcium antagonism demonstrated by Onkst and co-workers, sodium citrate was added as a chelating agent to sea water, to fresh water, and to distilled water containing 1 gm NaCl/l to determine what effect it might have on the induction of anesthesia in *Fundulus* (Figure 6). Examination shows citrate ion produced no change in the rate or depth of anesthesia in sea water (groups A and B). However, citrate increased both the rate and depth of anesthesia in fish adapted to fresh water (groups C and D), while in the groups adapted to fortified distilled water differences were negligible (groups E and F). The concentrations of calcium ion in ppm in the medium of all groups were: A, 352; B, 356; C, 12; D, 11.2; E, 1.6; and F, 1.6.[3]

The fact that calcium was essentially absent from groups E and F and low in groups C and D is in agreement with the conclusions of Onkst *et al.* (1957) for a calcium antagonism of sodium amytal anesthesia. The demonstration that calcium can inhibit the action of barbiturates explains the difficulties reported by Hara (1924) and Aitken (1936) when anesthetizing marine fishes.

The known role of calcium as an active agent for decreasing membrane permeability invites the interpretation that it affects passage of sodium amytal by decreasing per-

[3] Calcium was determined with a Beckman Model DU Flame Photometer. A direct method was used for samples C, D, E, and F, while the internal standard method of Chow and Thompson (1955) was used for samples A and B. Range of variation among samples was 3.5–4.0 per cent.

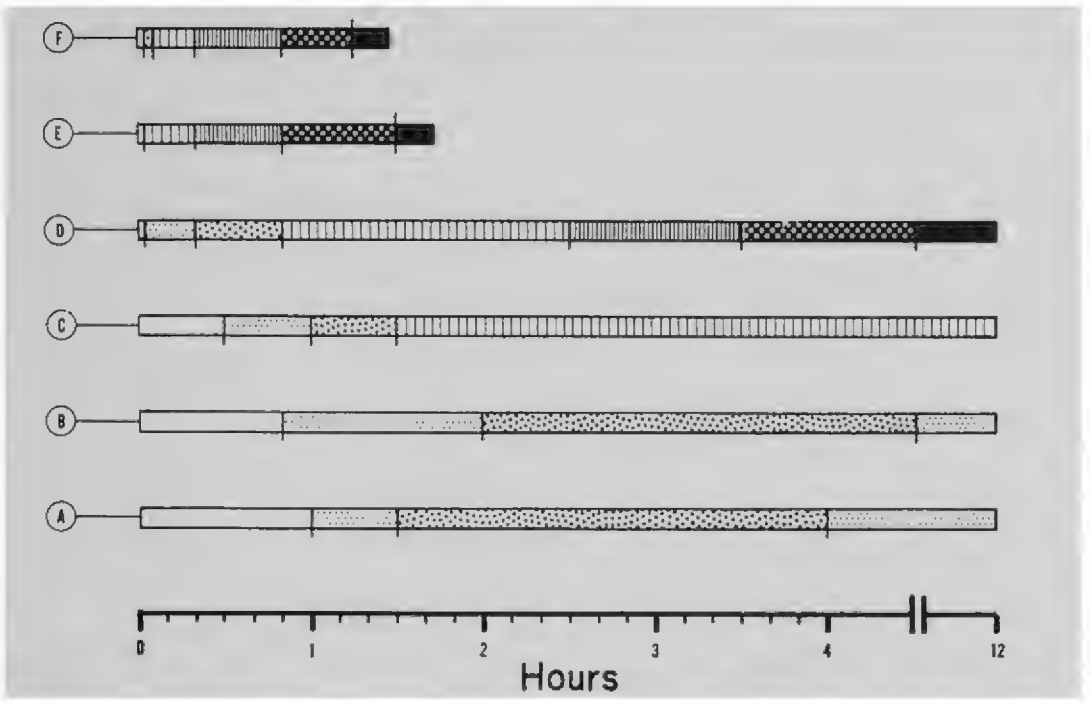

FIG. 6. The effect of sodium citrate on the rate and depth of sodium amytal anesthesia of *Fundulus parvipinnis*. Sodium amytal was used at a concentration of 3.0 grains/gal. (0.22 mM/l) in all groups. Groups A and B were in sea water, groups C and D in fresh water, and groups E and F in distilled water to which 1.0 gm of NaCl/l has been added. Groups B, D, and F were treated with 2.0 gm of sodium citrate/l. Each group was pretreated for six hours prior to introduction of the anesthetic. The abscissa, ordinates, and the coding system are the same as for Figure 1a.

meability across the gills. It is possible, however, that calcium interferes directly by forming a complex with sodium amytal which effectively decreases the rate of uptake from the medium. Whatever the mode of action, chelation is effective in increasing the rate of induction and the depth of anesthesia. In spite of its high narcotic potency, sodium amytal, and other barbiturates must be considered poor general anesthetics for fishes because of calcium antagonism. Their use is ineffective where water is not soft or where chelating compounds are not added.

The Relation Between Changes in Physiologic Functions of Fishes and the Stages of Anesthesia

Observations of behavior of fishes during anesthesia revealed that the rate functions often changed in a consistent manner. To establish a more exacting relationship the opercular rate, the pectoral fin rate, and the cardiac rate were determined for various depths of anesthesia. Each of these functions is described separately.

Opercular Rate

During anesthesia both the rate and amplitude of opercular movements are affected. As indicated in Figure 7, opercular rates for non-anesthetized *Fundulus* were mainly between 180–200 beats/min., although they ranged slightly above and below these values at various times throughout the 24 hour experimental period. The controls, therefore, maintained a relatively constant rate during the experiment. Both the control fish and the fish tested, prior to the introduction of the anesthetic, showed a slight tendency for the opercular rate to decline after introduction into the experimental vessels.

After the introduction of the anesthetic to the test vessels and during the induction of Stage I the opercular rate declined further (Figure 7). This decline was slight in the smaller *Fundulus* (from 185 to 170 beats/min.), but greater in the larger ones (from

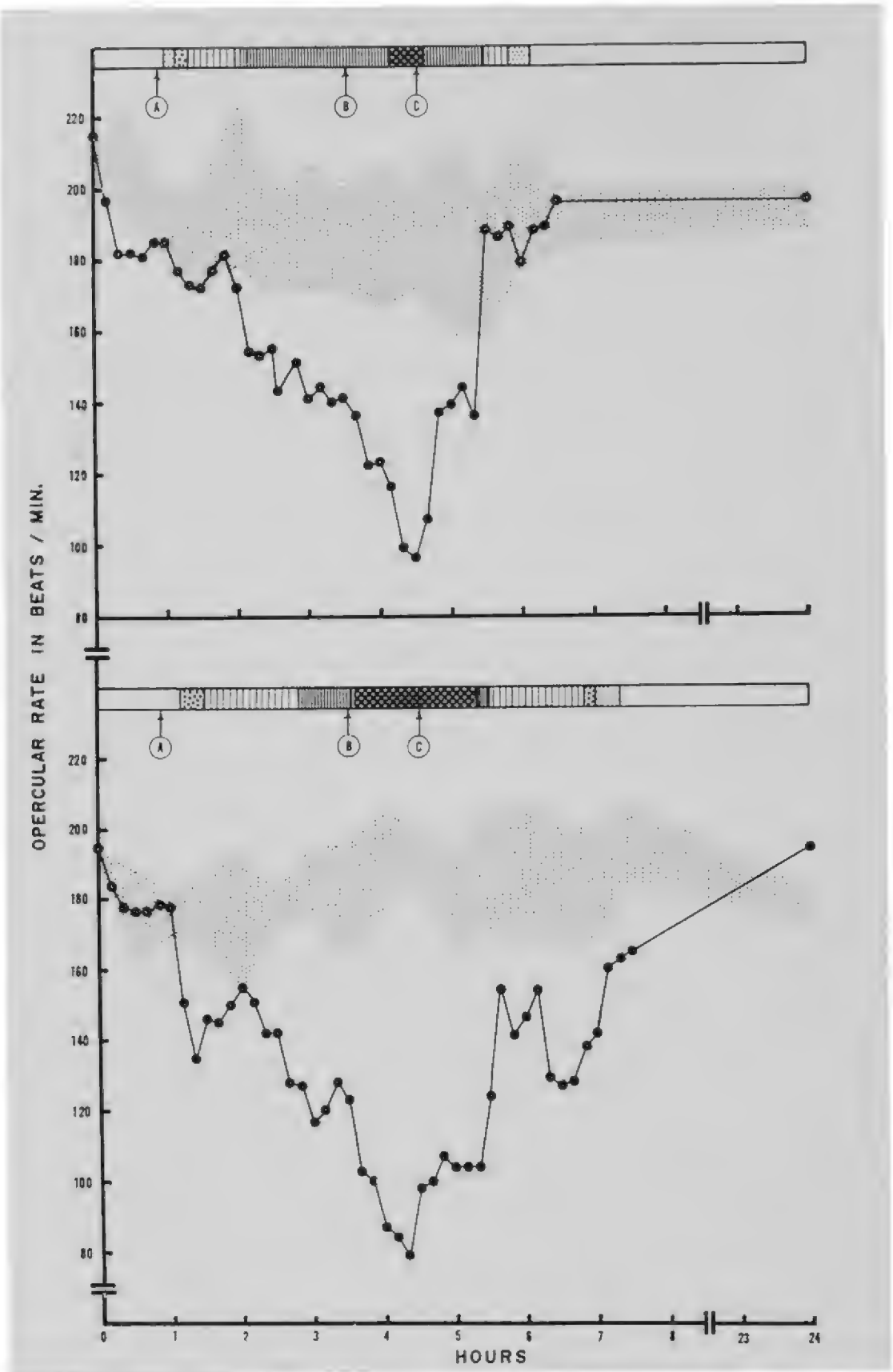

FIG. 7 The effect of anesthesia on opercular rate of *Fundulus parvipinnis*. The abscissa represents time in hours; the ordinate represents opercular rate in beats/minute. The stippled areas represent maximal and minimal rates among controls during 30 minute intervals. The black circles represent mean opercular rate of three anesthetized fish. Opercular rate was recorded every 10 minutes. Coded bars indicate the mean rate and depth of anesthesia, by means of symbols identical to those used in Figure 1a. The upper portion of the figure shows the mean rate for three *Fundulus* ranging in weight from 2.1–2.5 grams; the lower portion, the mean for three fish ranging in weight from 5.9–7.7 grams. Arrows indicate the time of administering anesthetic in each container; letters refer to anesthetic concentration. In both the upper and lower portion of the figure, A = 3 ml methylparafynol/gal. (7.3 mM/l) of sea water, B = 4 ml/gal. (9.6 mM/l) of sea water, and C = untreated sea water.

175 to 135 beats/min.). No noticeable change could be discerned in the amplitude of the opercular movements.

With the onset of Stage II-1, a slight, but noticeable increase in rate occurred in larger specimens followed by a decline during Stage II-2. In the smaller specimens the rate increased slightly, late in Stage II-1 and then declined steadily from 180 to 120 beats/min. with the induction of Stage II-2.

No change in the amplitude of the opercular movements was noted in Stage II-1 nor initially during Stage II-2. The amplitude visibly increased at the beginning of Stage III.

Stage III was associated with a further decline in the opercular rate (from 120 to/or below 100 beats/min.). The opercles were abducted a greater amount than normal during each beat and were not closed as completely during adduction. The branchiostegals were spread more than in normal fish, so that the opercular region appeared distended. This change was distinct and allowed definition of Stage III on criteria other than rate.

Similar changes in rate and movement of the opercles are associated with each stage of anesthesia during recovery. The relationships of opercular movements to anesthetic stage, however, are more difficult to correlate during recovery than during induction, since recovering fish often pass through the stages rapidly. The rapid increase in rate during Stage II-2 was also accompanied by a decline in the distention of the opercles (Figure 7). The decline in rate among the larger fish in Stage II-1 during recovery (Figure 7, lower graph), between six and seven hours, is believed analogous with the decline that occurs during the induction of Stage I. The apparent decline in rate in Stage II-1 during recovery, rather than with Stage I, is possibly due to the difficulty of defining stages precisely during recovery. Differential rates of diffusion of anesthetics from the various affected nervous centers may explain these differences. Recovery was complete in all the anesthetized specimens, the opercular rate being similar to the controls after 24 hours.

Similar results were obtained for *Girella nigricans* and for *Paralabrax clathratus*. In *Girella*, the increase in rate during induction of Stage II-1 was much greater than in *Fundulus*, the rate exceeding those of controls. Changes in amplitude of opercular movements in *Girella* were the same as in *Fundulus*. In *Paralabrax*, however, the amplitude of the beats becomes pronounced in Stage II-1 before the rate declines (see Cardiac Rate Experiments). The major changes in opercular rates and movements are seen to be related mainly to Stages II-2 and III.

Three other workers have reported changes in the opercular rate during anesthesia. In the flatfish, *Pleuronectes platessa*, Hara (1924), reported that all of the drugs he tested caused a reduction of about 50 per cent in the amplitude of opercular movements. Only sulfonal, trional, and adalin induced significant declines in rates (from 60–70 to 0–10 beats/min.) and severe changes in the amplitude of the movements (to 10 per cent of normal). Hara believed that different anesthetics were affecting respiration differentially at the same depth of anesthesia. In light of results of this study it seems more probable that he was actually measuring the rates for slightly different depths of anesthesia. This interpretation would account for the differences in rates and amplitudes he attributes to the different anesthetics.

In their study of the effects of sodium amytal on *Girella nigricans* and *Clinocottus analis*, Keys and Wells (1930) found that opercular movements increased slightly for several minutes after drug injection and then decreased abruptly to about one-half the normal rate (probably Stage II-2). The rate then declined further to about one-quarter the normal rate (probably Stage III) and remained constant for 5 to 10 hours. After this time it gradually increased to a normal level as the anesthetic wore off.

The major changes in opercular rates and movements, occurring during Stage II-2 and particularly in Stage III, indicate that the respiratory centers of *Fundulus* and *Girella* as well as of *Paralabrax* are resistant to anesthetic concentrations that upset other

central-nervous centers, affecting equilibrium, motor reactions, and sensory integration. The marked change in both rate and the amplitude of opercular movements is observed only after complete loss of equilibrium, loss of major motor responses, and loss of reactivity.

Pectoral Fin Movements in *Fundulus parvipinnis* and *Girella nigricans*

Pectoral movements varied among non-anesthetized *Fundulus* and *Girella*. Movement of the pectoral fins ordinarily ceases when the fish rests on the bottom.

Pectoral fin rates of non-anesthetized fish tended to be synchronized with opercular rates. The mean ratio obtained from division of the opercular rate by the pectoral fin rate for *Fundulus* was 1.002 (σ=0.14; n=160). The mean ratio for *Girella* was 1.023 ($\sigma = 0.20$; n = 250). With perfect synchrony a mean value of 1.000 would be observed. The close relationship between pectoral fin movements and opercular rate is particularly obvious when the fish hover. At this time it is apparent that each pectoral movement counteracts the thrust created by the effluent current from one opercular beat.

Some definite relationships exist between the depth of anesthesia and the pectoral fin movements (Tables 5 and 6). In *Fundulus* pectoral movements prior to anesthesia (Stage 0) are equally distributed between continuous movements or no movements, with a few erratic motions (Table 5). Movements are more equally distributed for *Girella* (Table

Table 5

Relationship between pectoral fin movements and anesthetic stage in *Fundulus parvipinnis*
Continuous fin movement refers to a rhythmic pattern; erratic fin movement to an interrupted pattern. Data are pooled from observations on six specimens, anesthetized with methylparafynol.

	Anesthetic Stage	Number of observations	Continuous fin movement	Erratic fin movement	No fin movement
Induction	0	40	18	3	19
	I–1	1	..	1	..
	I–2	10	6	1	3
	II–1	38	18	8	12
	II–2	54	8	5	41
	III	36		3	33
Recovery	II–2	25	1	2	22
	II–1	24	13	1	10
	I–2	5	2	..	3
	I–1	13	6	..	7

Table 6

Relationship between pectoral fin movements and anesthetic stage in *Girella nigricans*
Continuous fin movements refer to a rhythmic pattern, erratic fin movements to an interrupted pattern. Data are pooled from observations on six specimens, anesthetized with methylparafynol.

	Anesthetic Stage	Number of observations	Continuous fin movement	Erratic fin movement	No fin movement
Induction	0	60	34	13	13
	I–1	6	2	..	4
	I–2	15	33	..	12
	II–1	29	6	1	22
	II–2	19	..	..	19
	III	42	..	..	42
Recovery	II–2	21	1	..	20
	II–1	21	..	..	21
	I–2	4	..	..	4
	I–1	25	10	2	13

6). No marked deviation in the distribution of fin movements was observed during early anesthesia (Stages I-1, I-2, and II-1). However, continuous and rhythmic fin movements were strongly inhibited in Stage II-2 and ceased entirely during Stage III in both species.

The return of continuous fin movements during recovery is associated with emergence of *Fundulus* from Stage II-2 and emergence of *Girella* from Stage I-2. Pectoral fin movements during the induction of and the recovery from Stages I-1, I-2, and II-1 do not appear to be different. The tendency for fin movements to cease for *Girella* in Stage II-1 (Table 6) during induction and recovery as compared to *Fundulus* is unexplained.

The pectoral fins are almost always outstretched and held perpendicular to the body during Stages II-2 and III. It is not known whether the inhibition of pectoral movements is the result of uncoupling and/or a depression of central nervous centers or merely accompanies the general loss of muscle tone characteristic of these anesthetic stages. Further information relating pectoral fin movements to the depth of anesthesia has not been found in the literature, other than a description of synchrony between pectoral fin, tail, and body movements of *Carassius auratus* during early anesthesia (von Holst, 1934a & b).

Cardiac and Opercular Rates of *Paralabrax clathratus*

The effect of anesthesia on heart rate was measured in three kelp bass, *Paralabrax clathratus*, ranging from 200–250 gm. Methylparafynol was used as the anesthetic and introduced at intervals to increase the depth of anesthesia as determined by direct observation.

Respiratory collapse occurred in all of the kelp bass from 46 to 60 minutes after the first introduction of anesthetic. Since the electrograms contained tracings of both the cardiac and the opercular movements, changes in cardiac rates and opercular rates were easily related to anesthetic stage (Figure 8). Cardiac rate did not change drastically during anesthesia until late in Stage III (Figure 8). The heart beat was maintained for

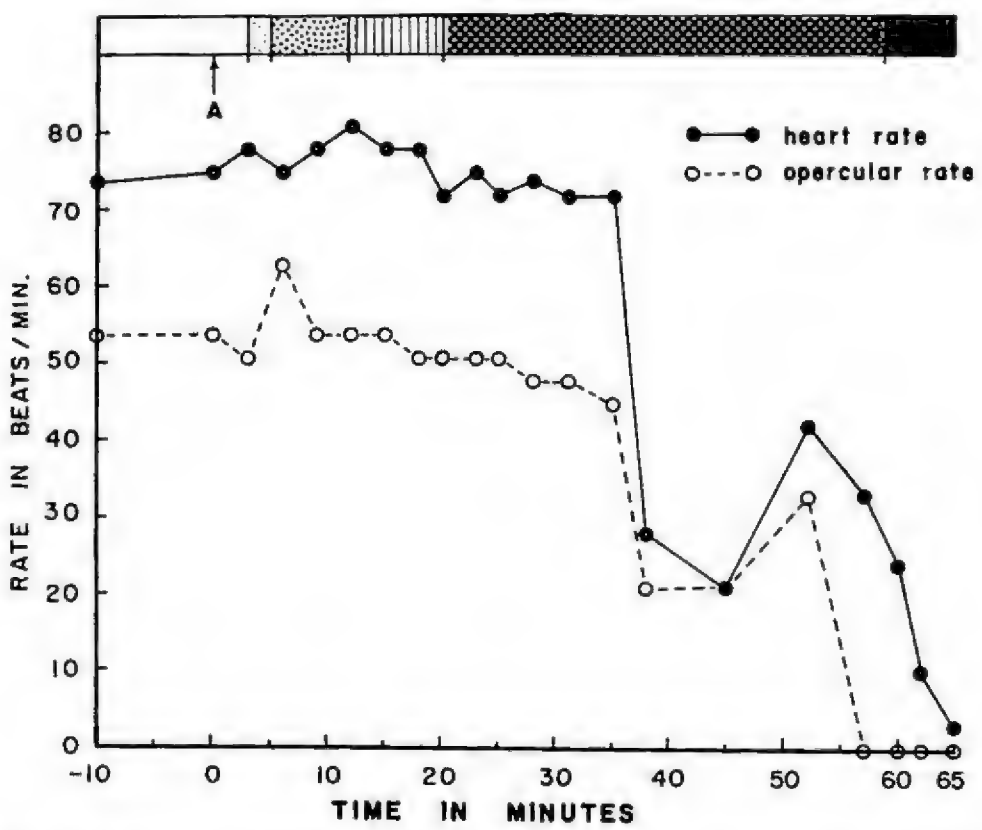

Fig. 8. The effect of methylparafynol anesthesia on the cardiac and opercular rate of *Paralabrax clathratus*. The coding symbols refer to the depth of anesthesia and are the same as those used and defined in Figure 1a. Change in rate for two other specimens did not vary significantly.

several minutes after the induction of Stage IV, declining to 5 to 10 beats/min. before collapsing abruptly three to five minutes after cessation of opercular movements. This delay in cardiac failure explains recoveries often observed for *Fundulus* and *Girella* in Stage IV after removal from the anesthetic. Heart rate tended to parallel opercular rate even late in Stage III, until opercular movements ceased. In fact, the ratio of heart rate to opercular rate for all specimens was quite constant, not varying greatly from 1.40 to 1.50 during anesthesia until late in Stage III and in Stage IV.

In addition to changes in rates, the tracings show other variations (Figure 9). First, the EKG is out of phase with the opercular rate in all specimens and in all stages of anesthesia, since the EKG shifts position with each opercular movement. Second, the amplitudes of both the EKG and the opercular wave decrease during anesthesia. The amplitude of the EKG decreases at Stage II-2 while the amplitude of the opercular wave first declines at Stage II-1 (not noticeable visually). Further changes in amplitude of the EKG do not occur until cardiac failure.

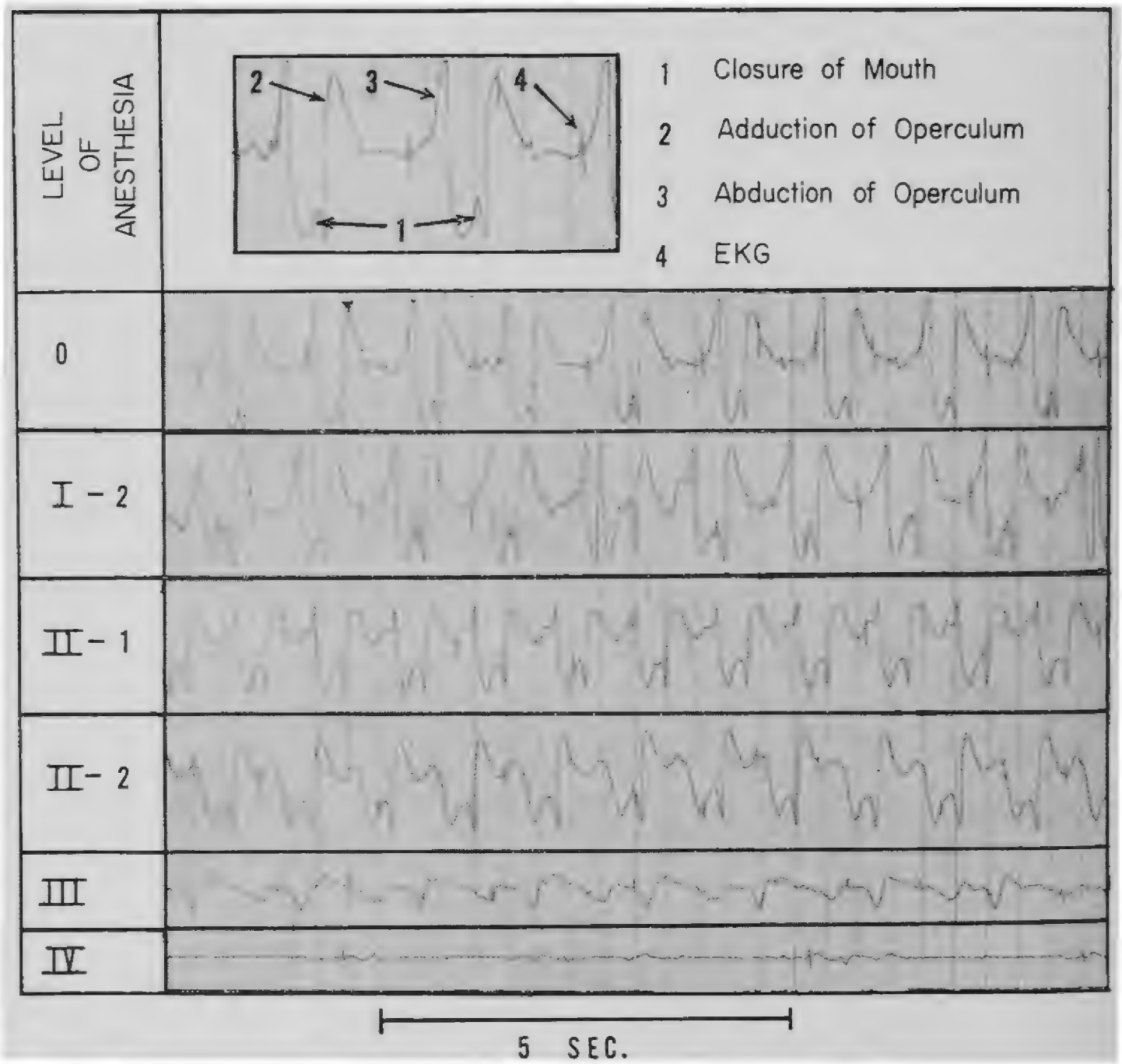

FIG. 9. The relationship between cardiac rate and anesthetic stage for *Paralabrax clathratus*. Tracings are arranged from top to bottom in order of increasing depth of anesthesia. The different waves are identified in the enlarged inset. Note that the EKG is not in phase with the opercular rhythm. The basic waves for the opercular potentials (waves 2 and 3) are maintained through Stage III: the differences shown with increasing depth of anesthesia represent changes in rate and amplitude of opercular movements. Only the EKG is discernible in Stage IV.

In the opercular wave are two major waves and a definable smaller one representing adduction and abduction of the opercles and closure of the mouth respectively. The shape of the opercular wave is not modified during the change in Stage II-1, but rather the adduction and abduction peaks are shortened. The abduction peak declines further in Stage II-2. However, the amplitude of the opercular wave is decreased markedly only in Stage III, in conjunction with declines in the opercular rate and the cardiac rate. The basic wave form persists until there is a respiratory collapse. The decrease in amplitude of the opercular wave in Stage II-2 and Stage III corresponds to the opercular distention described earlier for *Fundulus* and *Girella* during Stage III. The opercular wave is absent in Stage IV and is interpreted to indicate a complete medullary paralysis.

The results suggest that higher centers controlling cardiac and respiratory movements are loosely integrated. The delayed cardiac arrest is similar if not homologous to the respiratory and cardiovascular collapse during anesthesia of higher vertebrates, particularly man (Goodman and Gilman, 1955, p. 36). This persistence is most probably caused by local pacemakers and the myogenic nature of the vertebrate heart. Fibrillation, as in higher vertebrates, is common during cardiac failure (not shown in Figure 9). The decrease in the amplitude of the cardiac and opercular waves without basic changes in form is interpreted to signify a suppressive action of anesthetic (methylparafynol) on central nervous centers rather than a disruptive or lethal action.

Apparently similar information on heart rate for other fishes has not been ascertained.

Anesthesia and Metabolism

Individual metabolic rates of *Fundulus* in Stage I were measured using tertiary amyl alcohol, methylparafynol, chlorobutanol, and M.S. 222 as the anesthetic. During the course of the experiments three controls died and one was seriously upset, but no mortality occurred in the anesthetized groups. Three representative hourly plots of the metabolism of anesthetized and control *Fundulus* are pictured in Figure 10.

Oxygen was consumed at a high rate by most of the controls during the first two to three hours. However, high rates declined to more or less constant levels after four to six hours. On the basis of consecutive hourly readings, Ivlev (1938), Keys (1930) and Wells (1932) indicated declines in metabolic rate similar to those reported here for *Fundulus*. Keys and Wells both worked with *Fundulus parvipinnis* and showed similar declines that leveled off after about six hours. Wells also indicated a further, slower decline in metabolic rate over 24 to 48 hours.

It appears from these results (here represented only by Figure 10) that proper use of anesthetics to induce Stage I-2 can eradicate or greatly reduce the initial high rates resulting from handling. The greater variability in the metabolic rate of the 6.9 gm *Fundulus* (Figure 10) is probably due to the induction of Stage I-1 rather than I-2. Except with M.S. 222 more constant metabolic rates were found in anesthetized *Fundulus* than in untreated controls.

Induction of Stage I-2 also eliminated increases in metabolic rate caused by external stimuli. For instance, large increases occurred in the metabolic rates of the controls at 22 hours when stimulated by flashing lights, but no significant increases occurred in the anesthetized *Fundulus* (Figure 10). Also, when removed from the flasks at 23–26 hours, all the anesthetized fish were markedly sedated and did not react, with the exception of those treated with M.S. 222, which were as reactive as controls. *Fundulus* anesthetized

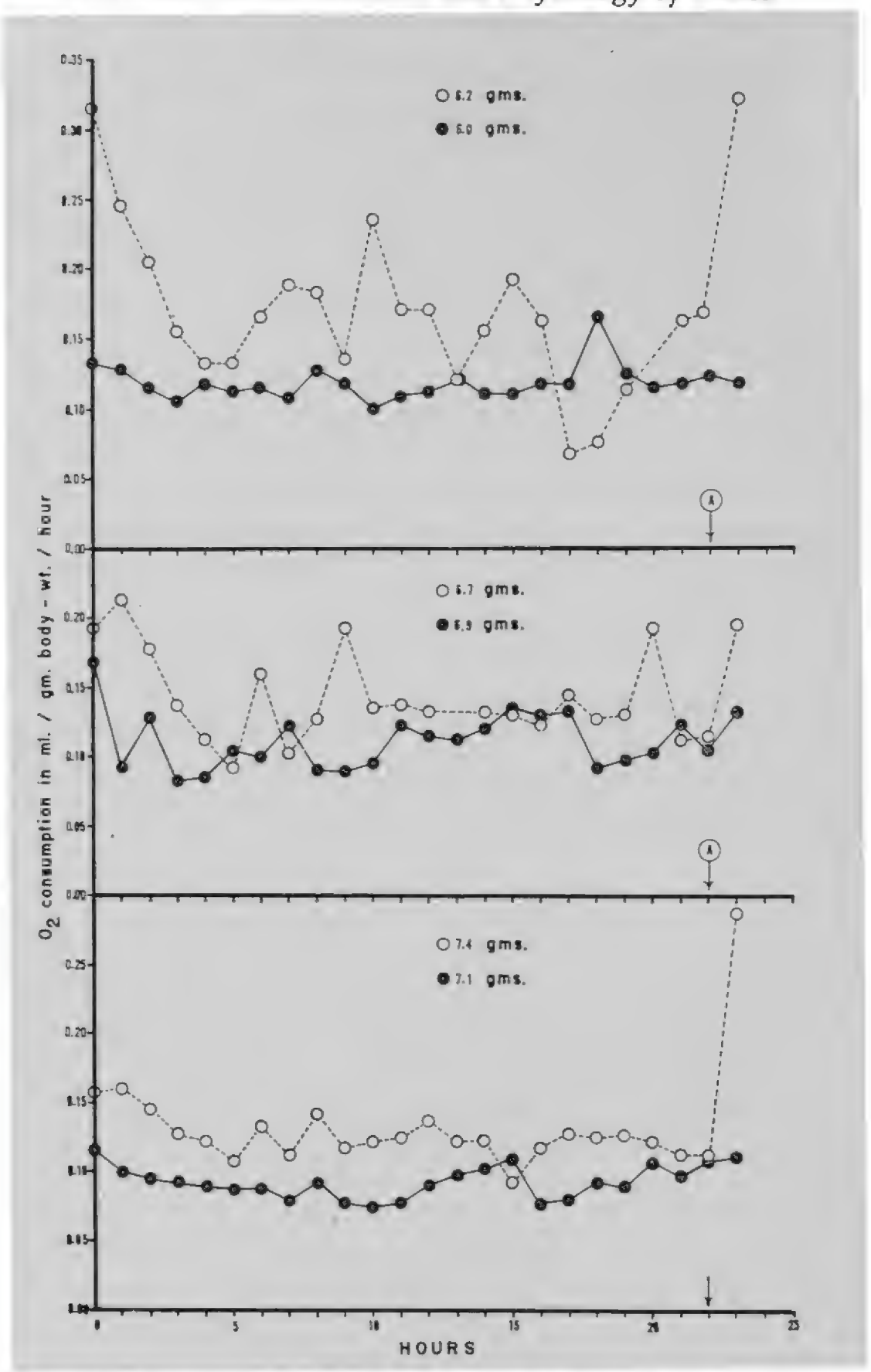

FIG. 10. The effect of chlorobutanol on the metabolic rate of *Fundulus parvipinnis* during 24 hours. Stage I-2 was induced with 1 gm chlorobutanol/gal. (~0.1 mM/l) of sea water. Paired curves (dotted and solid lines) are for *Fundulus* of similar weights. Solid lines and circles represent anesthetized fish; dotted lines and open circles represent controls. The upper, middle, and lower curves represent increasing size. All rates were measured in darkened Warburg flasks of 250 ml capacity. At 22 hours (point A) the cover was removed and the *Fundulus* excited by flashing the lights every ten minutes for one hour. Temperature during the experiment varied between 19.9°–20.1° C; acclimation temperature was 20 ± 1° C. Individual fish were pretreated for three hours with the anesthetic.

with M.S. 222 had oxygen rates similar to controls after six to eight hours. This similarity in rates may represent a metabolic breakdown of the M.S. 222 and a consequent reversal of the anesthesia.

Several changes in oxygen consumption that are directly related to anesthesia are of interest. The noted constancy in oxygen consumption of fish in Stage I-2 when compared with control fish (Figure 10) appears to be associated with different mean metabolic rates. The question arises as to whether the mean basal metabolic rates of the two groups

are the same or different. To test this question the regression of total oxygen consumed per fish on weight was compared for the control and anesthetized groups by analysis of covariance (Dixon and Massey, 1957, pp. 209–219). A significant difference between the means was found at the one per cent level of probability, but no difference was found between the slopes of the regression lines, although the slopes were different (slope of line for drugged fish, −0.86; for nontreated fish, −1.1). Comparison of the alpha coefficients of each regression line indicates that the basal metabolic rates of the controls were 34 per cent higher than that of the anesthetized groups.

The mean basal rate for the non-anesthetized fish (4 to 7 gm) was 0.133 ml O_2/gm body weight/hour (Stage 0, Figure 11) and 0.10 ml for anesthetized fish (same size range, Stage I-2, Figure 11).

Maximum oxygen rates for each individual fish during the period of stimulation (flashing lights) are shown in Figure 11. Activity rates varied for controls (Stage 0) but on the average were one and one-half to two times the basal rates and on one occasion almost four times the basal rate. Fry (1957) suggests the maximum sustained activity level for fishes (trout, goldfish, *etc.*) is usually four to five times the basal rate. Since the stimulus used was not maximal nor sustained, the values indicated in Figure 11 are of the order of magnitude that could be expected from Fry's findings.

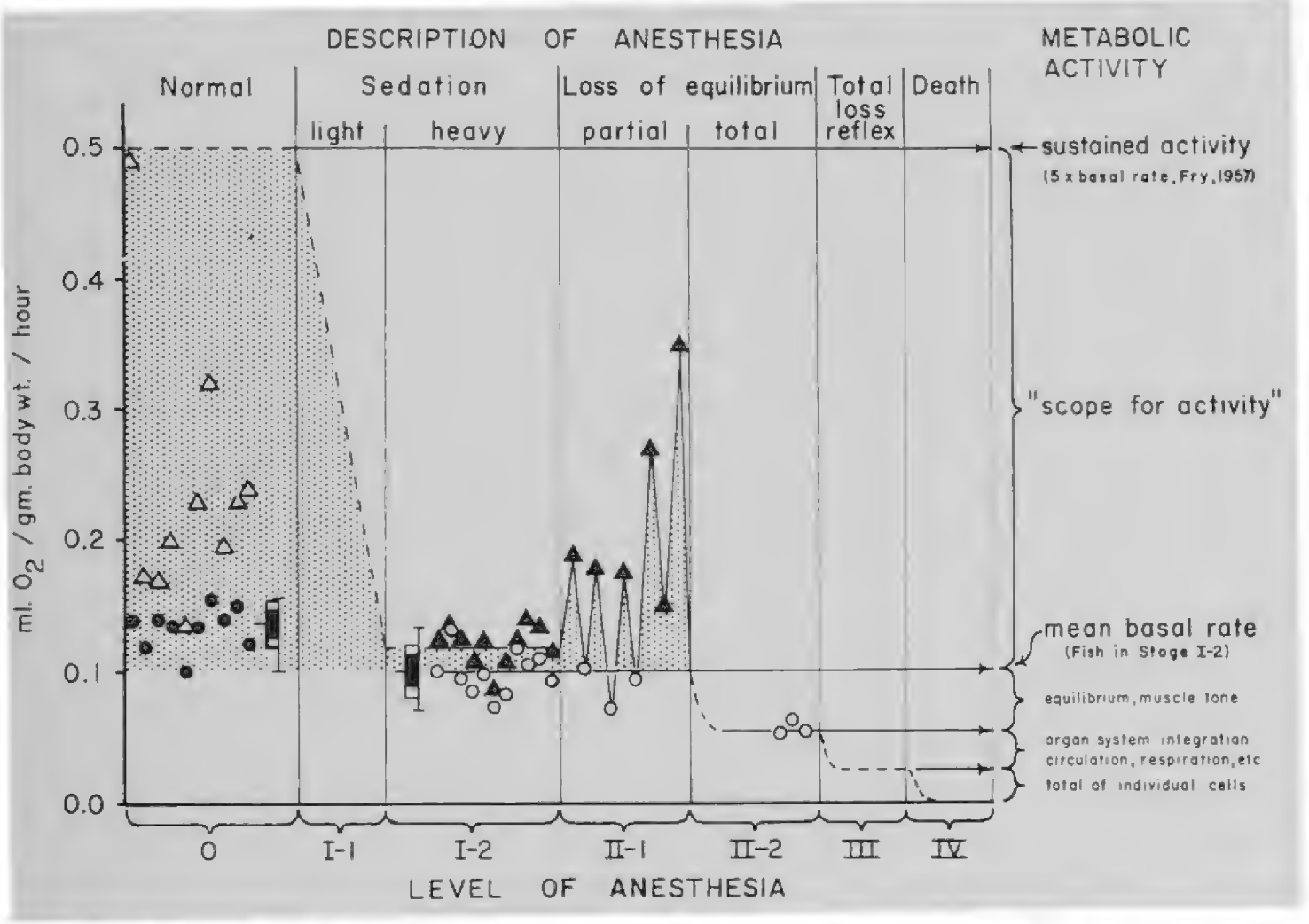

FIG. 11. Relationship between metabolic rate and the depth of anesthesia for *Fundulus parvipinnis*. The stippled area represents oxygen metabolism that can occur above the basal metabolism during each stage of anesthesia. The symbols are: black circles, Stage 0 = mean metabolic rates of undisturbed individuals; open faced circles, Stage I-2 and II-2 = mean metabolic rates of undisturbed individuals, Stage II-1 = low values obtained for undisturbed fish; open faced triangles, Stage 0 = highest values for stimulated individuals; and black faced triangles, Stage I-2 = highest values obtained for stimulated individuals, Stage II-1 = highest values obtained for undisturbed individuals. Dotted lines represent interpreted metabolic rates. Bars in Stages 0 and I-2 are statistical symbols drawn according to Hubbs and Hubbs (1953) and indicate a significant difference between the mean basal metabolism of non-anesthetized and anesthetized fish. Weights of individual fish varied from four to seven grams. Suggested individual components of fish metabolism are indicated in the metabolic activity column (see text for amplification).

The depression in reactivity induced during Stage I-2 is clearly demonstrated in Figure 11. Comparison of the maximum activity values of the anesthetized *Fundulus* with the maximum activity values found for controls indicates that the oxygen rate of each anesthetized fish is not more than 20–25 per cent greater than its basal rate and often much less. In fact, such variation can be considered normal and not the result of external stimulation.

The average metabolic rate in the first six hours after the fish is anesthetized (Figure 10) closely approximates the mean basal rate of each 22 hour trace. The results of Keys (1930) and Wells (1932) as well as those reported here clearly indicate that the first six hours should be ignored in calculating mean basal rates for fishes and also that variation thereafter can be considerable. In fact, the data in Figure 10 indicates that averaging only the bottom points of metabolic oscillations provides a better estimate of a basal metabolic rate than averaging the entire trace.

It seems clear from these results that anesthetics can be used effectively to measure basal metabolic rates of fishes. The drugs can be expected to increase the accuracy and reliability of basal metabolic measurements since they remove or greatly restrict the reactivity of fishes to external stimuli. It is not implied that accurate measurement of basal rates cannot be accomplished without anesthetics, but rather, that some of the usual critical precautions necessary can be eliminated (Fry, 1957, pp. 30–35).

The increases in oxygen uptake during Stage II-1 (Figure 11) agree with the observed tendencies of *Fundulus*, *Girella*, and *Paralabrax* to roll and to swim upside down. Indeed, the up and down rate graphed in Figure 11 is typical of hourly oxygen consumption records of *Fundulus* in this stage and correlates well with the observed but random periodic swimming, resting, swimming, *etc.*, before the fish enters Stage II-2.

Only three anesthetized fish were in Stage II-2 upon removal from the Warburg flasks. Data on these fish were obtained accidentally when the depth of anesthesia achieved exceeded that intended.

The decline in opercular rate during Stage II-2 can be considered a resultant from a lowered maintenance cost associated with loss of equilibrium and muscle tone. The opercular rate, however, although decreased, was still maintained at a relatively high level in *Fundulus* (Figure 7, 120 to 140 beats/min.) and in *Paralabrax* both the opercular rate and the cardiac rate were maintained during this stage (Figure 9). This suggests that blood and oxygen were being supplied to the tissues efficiently during this stage. Apparently irrigation of the gills is sufficient to supply oxygenation requirements. The fact that fish have been maintained in Stage II-2 for as long as 24 hours and the anesthesia reversed completely without apparent harm also indicates that basic transport functions to individual tissues were being maintained.

The mean value of 0.056 ml O_2/gm body weight/hour obtained for the three specimens of *Fundulus* (Figure 11) in this stage indicates that approximately 46 per cent of the basal rate is expended to maintain equilibrium and muscle tone (57 per cent of the mean rate of controls).

Oxygen consumption in both *Girella nigricans* and *Clinocottus analis* was found by Keys and Wells (1930) to decline to 40 per cent of the normal rate in deep anesthesia. Keys and Wells found the oxygen consumption to increase to 10 to 25 per cent above the normal rate as the effects of the drug (injected sodium amytal) wore off, an effect which they suggested was payment of an oxygen debt incurred during deep anesthesia. It is suggested, however, that the increased consumption was probably the result of an excess

activity during recovery resulting from the partial loss of equilibrium, which has been associated here with Stage II-1.

A further decline in metabolic rate is indicated in Stage III (Figure 11). The metabolic decrease may represent the cost of maintaining a fundamental integration of the organ systems including circulation, oxygen and carbon dioxide transport, *etc.* The diminished metabolism is reflected visually in the marked slowing and deepening of opercular movements (Figures 7, 8, and 9) and by a slowing in cardiac rate in Stage III (Figure 8). As with Stage II-2, Stage III has been maintained for long periods and anesthesia reversed. Such prolongation of deep anesthesia indicates that some lower metabolic rate is reached during Stage III. The exact rate of oxygen consumption depends on species, and the component of metabolism left may be considered the metabolic rate of non-integrated or non-stimulated tissues. Baudin (1932a, b, c, and d) found oxygen consumption declined to 25 per cent of its normal level during deep anesthesia (Stage III) in the goldfish, *Carassius auratus*, a value consistent with that suggested for *Fundulus* in Stage III.

Vernberg (1954) found the unit oxygen metabolic rate of brain brei to increase progressively from the sluggish toadfish, *Opsanus tau*, through the intermediately active scup, *Stenotomus chrysops*, to the active menhaden, *Brevoortia tyrannus*. Corresponding increases did not occur in other tissues. He concluded that a positive correlation exists between general activity and brain tissue metabolism as also found by others (Vernberg and Gary, 1953; Himwich *et al.*, 1939; and Freeman, 1950). If it is assumed that *Fundulus parvipinnis* is a fish of intermediate activity and that the percentage composition of its organ systems does not deviate drastically from the perch, *Perca flavescens* (Spector, 1956, p. 261), its overall summated basal metabolic rate would be 0.03 ml O_2/gm body weight/hour (allowing a Q_{10} correction of 2.5 for Vernberg's data; performed at 30°C). This estimate from tissue metabolism data agrees favorably with the results from anesthetized fish in Stage II-2 (less than 0.056 ml; probably 0.025 ml) and suggests that a considerable bulk of the maintenance metabolism is required to integrate the individual organ systems and to maintain balance and muscle tone.

It might be argued that decreases in cellular metabolism account for part of the decrease in metabolism of anesthetized fish during Stage II-2. The fact that high concentrations of anesthetic (6 to 44 times physiologic concentrations) are necessary to induce significant declines in the oxygen rate of brain tissues of mammals (Heilbrunn, 1952, p. 601) suggests that no major depression of cellular metabolism occurred. Nervous tissue is highly sensitive to anesthetics and apparently its activity is depressed without significant declines in oxygen uptake (Heilbrunn, 1952, p. 585). Even if the high unit metabolic rate of the fish brain (approximately 5 to 10 times the unit basal rate of the entire fish) were completely depressed during Stages II-2 and III, the depression of the summated metabolism would account for only about one per cent of the summated body oxygen rate since the brain constitutes only about 0.12 per cent of the body weight. The liver, heart, and gills would have to be included in the summation at the same high rate as the brain tissue to account for even one-half of the summated basal metabolic rate. It seems clear, therefore, that at least 50 per cent of the basal rate is required to maintain *Fundulus* in an integrated state. Thus, basal metabolism in a fish can be considered the result of at least three metabolic levels: cellular (tissue) metabolism, integrative metabolism of organ systems, and orientive metabolism (state of ready reactivity and maintenance of equilibrium).

Certainly more exacting measurements of oxygen consumption of whole organisms and tissues during deep anesthesia are needed. Most interesting would be the partitioning of basal metabolism, through anesthesia, of a sluggish, intermediate, and active fish. If Vernberg's conclusions are correct, orientive metabolism, or the maintenance cost of a state of ready reactivity, should be greater in the more active species. The cellular and integrative metabolism should be affected to a lesser extent in all three species. Therefore, one might expect greater relative declines to occur in the basal metabolic rate of the active species when deeply anesthetized.

Comparison of Anesthesia in Fishes and in Humans

Anesthesia in fishes may be compared with anesthesia in higher vertebrates, particularly man. In Table 7 the stages herein defined for fishes have been correlated with those proposed for man by Guedel (1951) and Harris (1951). A remarkable parallelism exists.

Of the four stages defined by Guedel for man and the four stages here defined for fishes, two appear to be virtually identical. Stages I and IV of both classifications are characterized by similar basic changes in behavior, *i.e.*, quiescence and depression of the medulla oblongata. Stages II and III of Guedel's classification are more difficult to equate with those proposed for fishes, although both have several features in common. Guedel's delirium stage is characterized by increases in skeletal muscle tone, involuntary motor activity due to the release of lower motor centers through a paralysis of higher centers, and irregular and increased respiration. Similarities are seen in fishes in the partial loss of equilibrium, uncoordinated swimming, and increases in the opercular rate during Stage II-1. Whether there is a corresponding increase in skeletal muscle tone in fishes during this stage has not been demonstrated. The end of Stage II-1 in fishes is felt to be equivalent to the end of Stage II in Guedel's classification.

The end of Stage II and the beginning of Stage III-1 in humans is characterized by an abrupt beginning of rhythmical respiration. This change has no exact counterpart in fishes since opercular movements have been shown to vary during Stage II-2 in different species. Further, parallels between the respiratory reactions of fishes and higher vertebrates during anesthesia are not homologous, nor should they be expected to react identically since different motor systems are involved in respiration. The onset of Stage II-2 in fishes is considered analogous to the onset of Guedel's Stage III-1, because of a flaccidity of the skeletal muscles when equilibrium is totally lost and the decrease in the amplitude of the heart beats (Figure 9). The muscles become flaccid, movement patterns cease, and there is a decline in the pulse rate and blood pressure in humans during Stage III-1. However, respiration is maintained at a high level. A high opercular rate is maintained during Stage II-2 in *Paralabrax*, but not in *Fundulus* and *Girella*. The only phenomenon primarily common to this depth of anesthesia in fishes and humans appears to be the muscle flaccidity.

Stage III in fishes is believed to be equivalent to Guedel's Stage III, planes 3 and 4. A total loss of reflex reactivity is common in both forms and respiration collapses toward the end of the stage.

In his classification, Harris equated each behavioral level of anesthesia with suppression of a particular central nervous center (see footnotes, Table 7). It is possible to suggest which central nervous centers may be suppressed at each anesthetic level in fishes

TABLE 7

A comparison of the sequence of anesthesia in humans and fishes

Classification of Ether Anesthesia in Humans (Harris, 1951)		Classification of Anesthesia in Humans (Guedel, 1951)		Suggested Classification of Anesthesia in Fishes		
Stages	Sub-stages	Stages	Planes	Stages	Planes	Possible CNS centers effected
Depression of the highest centers	Amnesia*	I	Analgesia	I	1	Depression of telencephalon
	Co-operative stupor†				2	Depression of sensory areas of tectum and tegmentum
	Non-cooperative stupor‡	II	Delirium	II	1	Complete depression of midbrain and thalamus
	Anesthetic sleep§	III	1 Sleep			
Depression of areas of sensory co-ordination¶	Loss of the ability to react to external stimuli		2 Sensory loss		2	Depression of the cranial sensory nuclei
Depression of areas of motor coordination‖	Small muscle groups		3 Loss of muscle tone	III		Depression of motor nuclei of the medulla and of the spinal reflex arcs
	Large muscle groups intercostal muscles		4 Intercostal paralysis			
Depression of the vital medullary centers#	Failure of the respiratory center	IV	Medullary paralysis	IV		Depression of the respiratory center
	Failure of the vasomotor center					Depression of the cardiac center
	Failure of the cardiac center					Cardiac collapse

Equation of anesthetic stages with depression of specific components of the CNS of humans (Harris, 1951): * depression of frontal association areas of cerebral cortex; † partial depression of sensory association areas of cerebral cortex, neocerebellum, and flocculo-nodular lobes of cerebellum not sufficient to release the hypothalmus and thalmus from inhibition; ‡ complete depression of cerebral cortex and release of hypothalmus; § complete depression of hypothalmus and upsets in integration of proprioceptive messages by thalmus and vestibular nuclei; ¶ complete depression of thalmus and all cranial nuclei, allowing reaction only to intense proprioceptive stimuli; ‖ complete depression of motor nuclei of the cerebellum, medulla, and interference with spinal reflex arcs; # complete depression of respiratory, vasomotor, and cardiac centers.

by comparing the human anesthetic pattern with what is known concerning the functions of the fish brain. For instance, Healey (1957) indicates that ablation of the telencephalon is associated with slight decreases in the response of fishes to stimuli, a condition similar to that which characterizes Stage I-1. This condition is strikingly analogous to Harris's sub-stage of *amnesia* for humans, a condition that he relates to a depression of the frontal areas of the cerebral cortex.

The tectum of fishes is believed to perform a non-rational, but otherwise similar role to that of the cerebal cortex in higher vertebrates. A partial suppression of the sensory areas of the tectum of fishes and thalamus may explain the total loss of reactivity charateristic of Stage I-2 and can be related to the sub-stage of *cooperative stupor* in humans.

The complete depression of the cerebral cortex that is associated with *non-cooperative stupor* in humans has its counterpart in the complete suppression of the tectum in fishes (Stage II-1). Whether this actually occurs in fishes is problematical, but the demonstration that partial or total ablation of the tectum and tegmentum is followed by upsets in swimming balance (Healey, 1957, pp. 16–18) strongly suggests such an analogy.

If Stage II-2 of fishes is caused by a suppression of the nervous centers that Harris associates with *anesthetic sleep* and *depression of sensory co-ordination*, it might be postulated that depression of all the cranial sensory nuclei causes the loss of muscle tone as well as the complete loss of equilibrium in fishes. Bilateral extirpation of the labyrinthyn organs of fishes does result in a temporary or lasting loss of muscle tone (Lowenstein, 1957).

Stage III of fishes may be compared with the stage of *depression of areas of motor co-ordination* for humans since a depression of motor nuclei of the medulla may lead to observed decreases in the power of opercular contractions (Figure 9). Furthermore, the loss of reflex reactivity to strong stimuli so often demonstrated in fishes may be caused by a depression of the spinal reflex arcs.

As in Guedel's classification, the *depression of the vital medullary centers* controlling respiratory and cardiac movements also are found in Stage IV in fishes and the centers are suppressed in the same sequence. In fishes, as in higher vertebrates, behavioral reactions to anesthetics indicate that the nerve cells are the most sensitive and thus the first to be suppressed.

It has been demonstrated by Tiffeneau *et al.* (1933) and Tiffeneau and Broun (1935 and 1937), that the bromide concentration in the brain tissues of several fresh water fishes when anesthetized with tribromoethanol or propyl bromide were identical at equal depths of anesthesia (Stage III). In addition, the bromide concentrations in the brain were found to be distinctly higher than in other parts of the head. Similar findings are reported by Lindenberg and Gary-Bobo (1951). Electrophysiological evidence as yet has not been obtained, the above papers representing the only direct evidence of CNS suppression during anesthesia in fishes. Nevertheless, the striking parallel of anesthesia in fishes and higher vertebrates, as well as a basic morphological similarity of the nervous systems, leaves the impression that fundamental processes in anesthesia are produced through a suppression of neural centers, which, if not morphologically homologous, are at least in part, functionally equivalent.

Summary

1. The effects of 21 chemicals were tested on the teleosts, *Fundulus parvipinnis* and *Girella nigricans*, and to a lesser extent on *Paralabrax clathratus* and *Gambusia affinis*. Fifteen of the chemicals were found to have anesthetic properties, while five had no visible effect or were toxic.

2. Behavioral changes during anesthesia are described for *Fundulus* and *Girella*. Behavioral changes are similar for both species and follow the same sequence. This behavioral sequence is independent of the anesthetic. Levels of anesthesia are classified on the basis of the behavioral changes described and four progressive stages of anesthesia are adopted. The four levels represent sedation, loss of equilibrium, loss of reflex reactivity, and medullary collapse.

Comparisons are made with previous descriptions of anesthesia of fishes and with

classifications of anesthesia for humans. Behavioral changes are equated and it is concluded that anesthesia is a common process in vertebrates and is effected by a sequential suppression of higher to lower central nervous centers.

3. Results from dosage experiments reveal that the narcotic potency of anesthetic compounds increases with increasing molecular weight for fishes. Tribromoethanol, with the highest molecular weight, was the most potent anesthetic used (approximately 1350 times as potent as ethyl alcohol), while ethyl alcohol was the least potent. It is shown that a particular depth of anesthesia can be maintained for long periods by controlling the concentration of anesthetic in the medium. Total tolerance to anesthetics for a fish is shown to be of the order of from 10 to 15 times the minimal dose, while doubling the dose will generally increase the depth of anesthesia by one level (stage or plane).

4. The size of fish is shown to affect both the rate and depth of anesthesia, smaller fish being more resistant. The temperature of acclimation of fishes also affects the rate of induction of anesthesia and causes a two- to three-fold decrease in induction time for a 10°C increase. A calcium antagonism of anesthesia, induced with sodium amytal, is demonstrated. Chelating agents are shown to be effective in partially combating this antagonism in fresh water, but not effective in sea water.

5. Opercular movements and pectoral fin movements for non-anesthetized *Fundulus* and *Girella* are found to be synchronous. This synchrony is affected only during deep anesthesia, when the pectoral fin movements cease and the opercular movements decline in both rate and amplitude. Cardiac rates and opercular rates, measured for *Paralabrax clathratus,* were found to be in loose synchrony and were not seriously disrupted until deep anesthesia was induced.

6. Basal metabolic rates of *Fundulus* were measured under mild anesthesia and a significant decline found in comparison to controls. This decline is attributed to a lowered reactivity to external stimuli. It is concluded that careful induction of mild anesthesia (sedation) can give reliable basal metabolic measurements for fish without the necessity of extreme precautions. In addition, the effect of anesthesia on basal and activity metabolism for each stage of anesthesia is discussed. On the basis of these results the basal metabolism of *Fundulus* is partitioned into three major components, *viz.*, individual cellular or tissue metabolism (non-integrated); organ system (partly integrated); and orientative metabolism (state of ready reactivity or totally integrated metabolism). The cost of maintaining equilibrium and a state of ready reactivity accounts for at least 50 per cent of the basal metabolism.

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Studies on the Hydrography and Fish Migrations of Cedar Bayou, A Natural Tidal Inlet on the Central Texas Coast[1]

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Abstract

Cedar Bayou Pass, a natural tidal inlet on the Texas Coast, was the subject of studies in 1950–1951 and 1957–1958. In 1950–1951, when the pass was open, it was utilized extensively by fishes, crabs, and shrimp as a passageway to and from the Gulf of Mexico. Most movement was nocturnal and more fish moved to the gulf than to the bay. The fish taken in largest numbers was the Atlantic croaker which migrated gulfward during summer months. Sea trout were frequently captured but these were normally following schools of shrimp. Outward movement of southern flounder was intense during fall months but the expected heavy migration of redfish and black drum did not occur.

In 1957–1958, when the pass was closed, many of the same species were found. These normally appeared at a later date than when the pass was open. Many typical gulf species were not present in 1958.

It is suggested that discharge from the Guadalupe River, together with northers, is responsible for maintaining this inlet and that it is prone to close during periods of drouth.

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Introduction

Since the beginning of serious concern about the marine fisheries of Texas, the subject of the "fish pass" has been prominent. Fish passes are small inlets between estuarine lagoons and the open gulf through which fish may pass enroute to breeding or feeding areas. Much controversy has developed concerning the importance of such passes to fish populations. Inlets have received little study and there is much speculation on the effects of inlets on the production of harvestable stocks (Hoese, 1958).

The object of this paper is to present information on the ecology and hydrography of Cedar Bayou, a natural tidal inlet on the Central Texas Coast, connecting Mesquite Bay with the Gulf of Mexico by means of a narrow slough three miles in length (Figures 1 and 2). This paper includes studies made in 1951–1952 when the pass was open, and data in 1957–1958 when the pass was closed. Stations occupied in the later study are shown in Figure 2.

Acknowledgments

These studies were supported by the Texas Game and Fish Commission. Work done by Simmons in 1950–51 was started in 1949 by Mr. W. L. Haskall, Biologist, under the supervision of Mr. J. L. Baughman, former director of the Marine Laboratory, Texas Game and Fish Commission. Work done by Hoese in 1957–58 was submitted to the Agricultural and Mechanical College of Texas as part of the requirement for the Master's degree (Hoese, 1959). The Marine Laboratory at Rockport, Texas served as a base for operations and its staff provided field labor as well as other assistance. Dr. Sewell H. Hopkins supervised the 1957–58 work on Hoese's thesis and his assistance and criticisms are gratefully acknowledged. Dr. E. Alan Lohse assisted with the geologic aspects and Dr. R. O. Reid critically analyzed the hydrography section. Dr.'s H. Hildebrand and William McFarland criticized the manuscript. Mr. Trigg Twichell, of the U.S. Geological

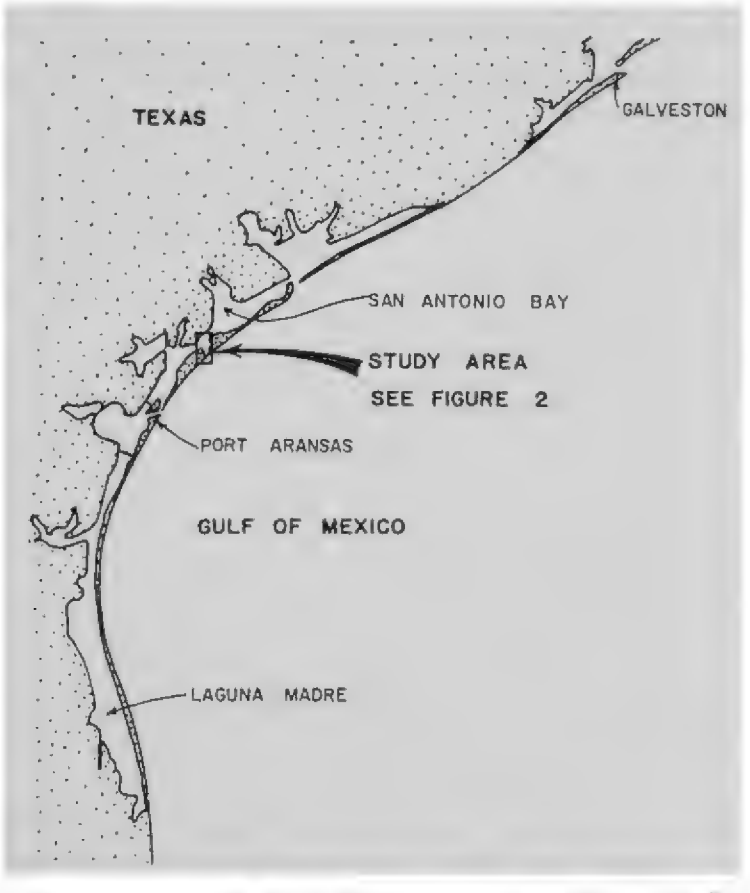

Fig. 1. Northwestern Gulf of Mexico showing Mesquite Bay area.

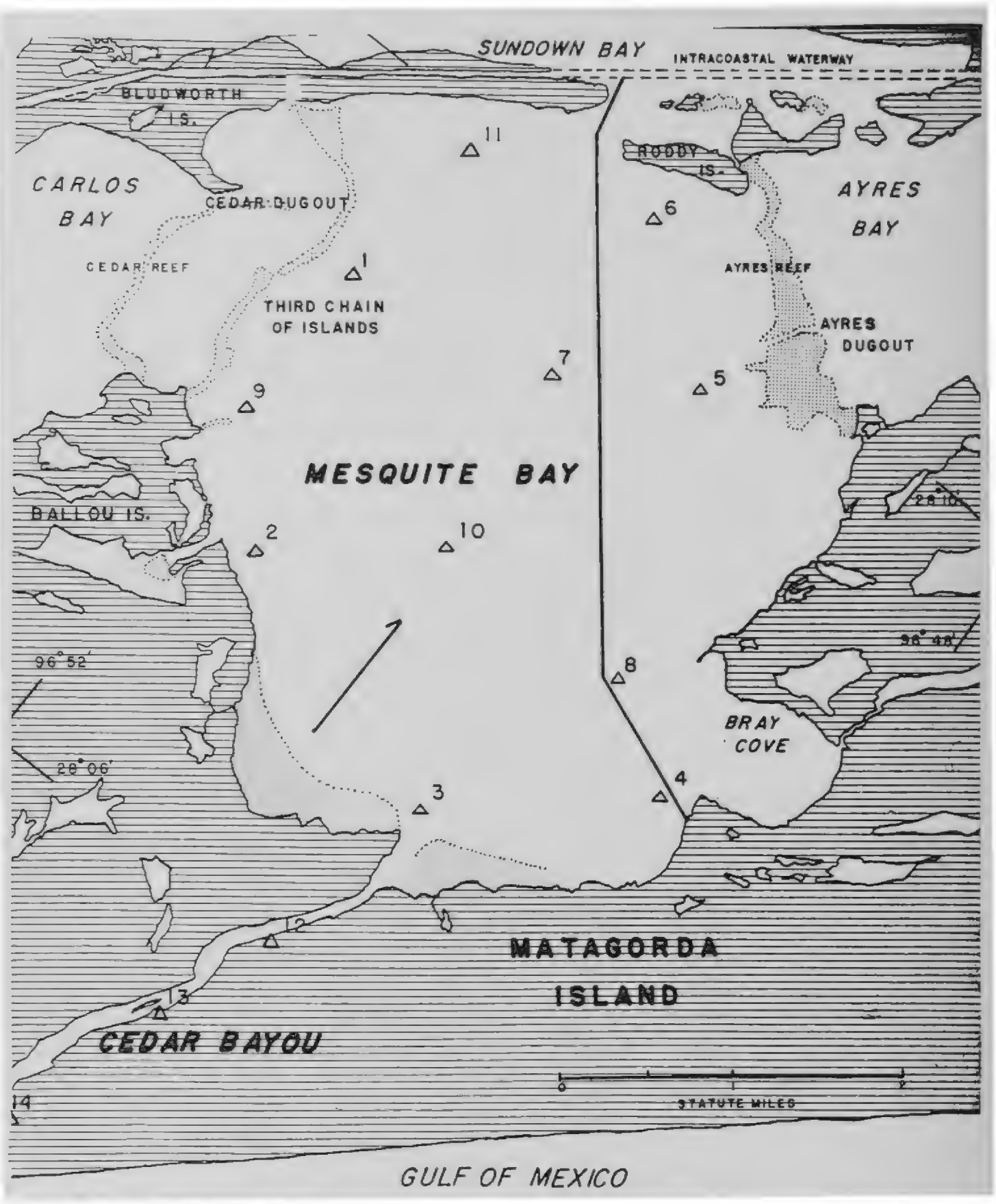

FIG. 2. Mesquite Bay and Cedar Bayou showing major features and stations occupied in 1957–1958 study. Line from Sundown Bay to Bray Cove represents channel discussed in text.

Survey, supplied unpublished river discharge figures. Mrs. Virginia Dickey and Miss Sandra Pounds drew most of the figures.

PREVIOUS STUDIES

Only one published study has been directly concerned with the biological effects of a gulf inlet (Reid. 1955a and b, 1956a, and 1957). Reid (1956a) found (1) quantitative changes in species populations and (2) apparent immigration of stenohaline marine forms after the opening of an inlet into East Bay, Texas. These effects were presumably due to the introduction of more saline water through Rollover Pass. After the partial

blocking of the inlet (Reid, 1957), the bay was found to be reverting toward conditions of species populations found before the inlet was constructed. Another study revealed the movement of two bay fishes through the newly constructed pass to nearby gulf beach areas (Reid, 1956b).

Whitten, Rosene, and Hedgpeth (1950) have studied the invertebrate fauna of jettied inlets on the Texas Coast, but the fish fauna of the jetties remain to be studied. Redfield (1952) has discussed some effects of opening and closing of an inlet on the oysters and hydrography of Moriches Bay, New York.

Methods

During the period from March, 1950 to June 10, 1951 an attempt was made to determine the role played by Cedar Bayou, then open as a fish pass. Fish traps were installed so that organisms moving toward the bay would be captured in one trap while those moving toward the gulf would enter another. Grass Island was used as a base of operations. Fences were installed running southeast from St. Joseph's Island and northeast from this shore to a point near Grass Island (Figure 3). At this point frames were built and within these removable trap boxes were installed. Long lead fences were also constructed at angles from Matagorda Island to Grass Island. Later a spiral type trap was installed on the gulf side, which proved more effective than the original trap.

This was a difficult area in which to maintain equipment; consequently, considerable time was spent in repair work. Fences were washed out frequently and wood borers destroyed many pilings. Many fish escaped through holes washed under the fences.

A biologist and crew stayed with the traps each week from Monday until Friday. Both trap boxes were lifted at 8:00 A.M. and 6:00 P.M., thus giving information on diurnal and nocturnal movements. Early attempts were made to correlate catch with tidal flow.

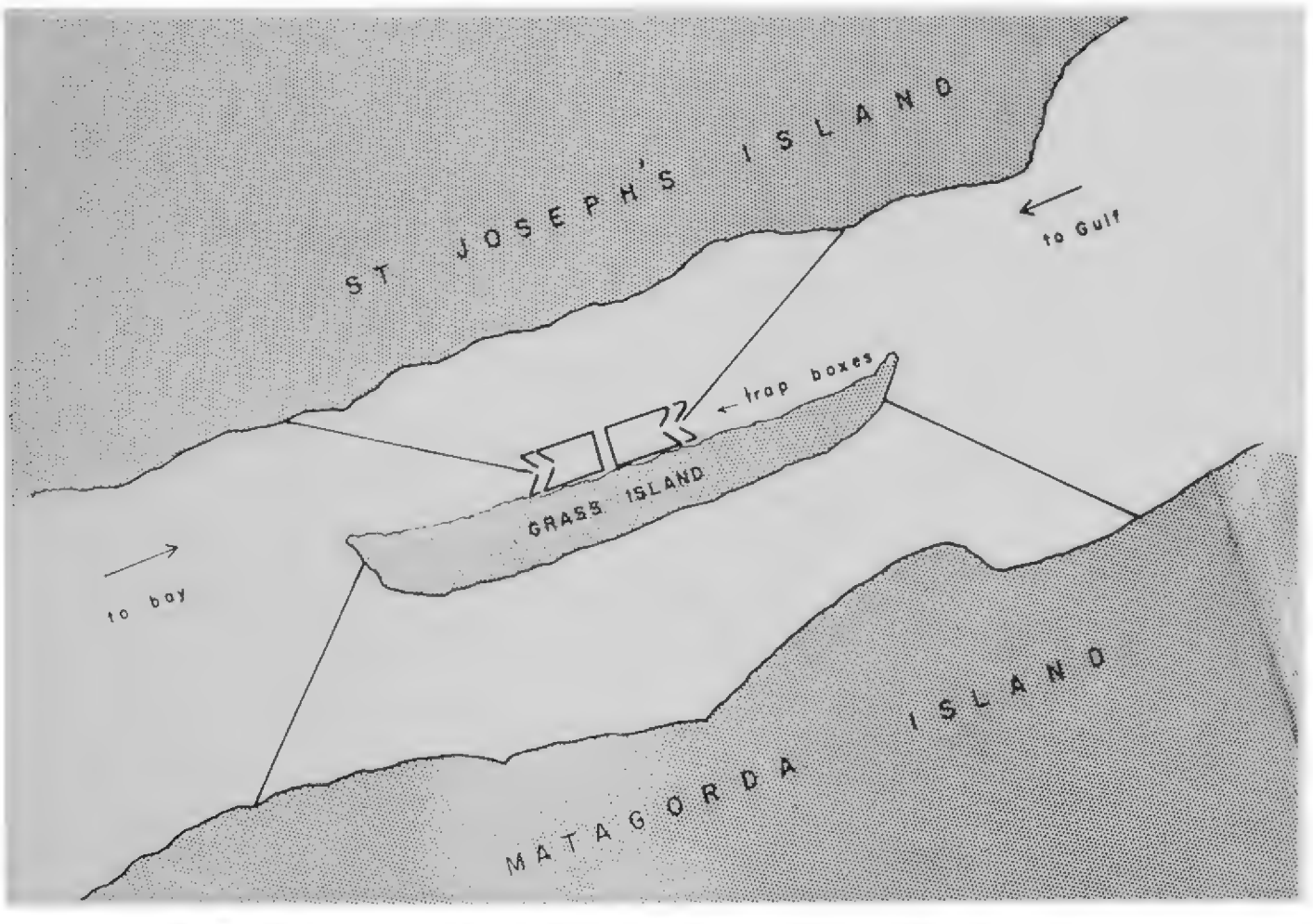

Fig. 3. Grass Island area showing fish trap used for 1950–1951 study.

However, this was later discontinued. All fish and crabs were counted and movements of shrimp were noted. Fish were carefully checked to determine if they were sexually mature, and a tagging program was established as an aid in studying movements and migrations. Trammel nets were used to supplement trap sampling. The data have been presented in mimeographed form (Simmons, 1950 and 1951).

Studies in 1957–1958 were based mainly on one collection per month at each station (Figure 2) at approximately monthly intervals with a ten foot otter trawl. The trawl had 1.75 inch stretched mesh and was pulled in a circle for ten minutes behind an inboard boat.

Otter trawls, gill nets, trammel nets, seines, dip nets, and hook and line were used to sample species not normally taken in trawls. Mollusks were sampled with an Ekman dredge and with oyster dredges.

Salinities, except where specified, were determined by the Mohr method (silver nitrate titration) and presented as total dissolved salts in parts per thousand. Thermometer temperatures were read to 0.1°C. Hydrographic data were obtained at least once a month at each station, besides those taken during the trawl sampling, so at least 28 values are available for every month except December during the main study. A Beckman model G pH meter was used to measure hydrogen ion concentration. Turbidity was measured from water samples with a Lumitron Colorimeter, using distilled water as a standard in tubes with an 18 mm outside diameter. These values are expressed as percentage light transmission. River discharge figures were taken from surface water supply papers for the Western Gulf of Mexico and unpublished data of the U.S. Geological Survey. River discharge is expressed as cfs (cubic feet per second flow). All measurements of fishes are standard length. Shrimp were measured by rostrum-telson length and crabs by carapace width.

Physiography of the Mesquite Bay-Cedar Bayou Area

Mesquite Bay is located at about 96°50′W., 28°10′N. (Figure 1). The center of the bay is 24.8 miles from Aransas Pass (the pass) and 30.6 miles from Pass Cavallo.

This is a small, oval, partly occluded bay, separated from Aransas and San Antonio Bays by two smaller bays and by chains of oyster reefs (Figure 2). The long axis of the bay is perpendicular to the Intracoastal Waterway in this area and is 4.6 miles in length. The greatest width is 3.8 miles. The area is 13.5 square miles (Collier and Hedgpeth, 1950). The basin is shallow with a saucer-shaped profile. U.S. Coast and Geodetic Survey maps list the maximum depth as 4.5 feet at mean low tide.

At one time the Intracoastal Waterway ran through Mesquite Bay, entering from the northeast through Ayre's Dugout and leaving to the southwest through Cedar Dugout. The present channel through Sundown Bay was dredged in April, 1940 and was widened and deepened in November, 1943. A channel from Sundown Bay runs through Mesquite Bay to Matagorda Island near Bray Cove. This channel is now evident only by a set of posts.

The bay is located between two washover fans (Shepard and Moore, 1955; Figures 4 and 5) each containing many small bodies of water and marshes.

Cedar Bayou, a natural, three mile long tidal inlet, originally connected Mesquite Bay with the Gulf of Mexico (Figure 4). In 1955 it shoaled at the gulf mouth and has been closed most of the time since. Prior to that time it separated Matagorda Island on the east from St. Joseph's Island on the west. This inlet is deeper than Mesquite Bay with

FIG. 4. Gulf mouth of Cedar Bayou on December 17, 1956 showing areas of deposition and erosion. Mesquite Bay and washover fan is visible in background.

FIG. 5. Gulf mouth of Cedar Bayou while closed showing Vincent's Slough and washover fan on St. Joseph's Island.

depths of six feet not uncommon and with places as deep as nine feet. However, the depth near the gulf was usually not over two feet while open.

Near the center of this passageway lies Grass Island, a small bar about 840 feet long and 125 feet wide. On the west side of this island is the main channel which is 140 feet wide; on the east is an area of shallow water 160 feet in width. Approximately one mile from the gulf a large mud flat begins on the east shore and extends nearly to Grass Island. On the west shore is Mud Slough, a fairly deep cove with bottom composed of mud, sand, and dead oyster shell. Beyond Grass Island, toward Mesquite Bay, lie more sand and mud flats and a few small reefs. Large oyster reefs and sand bars mark the merging of the inlet with Mesquite Bay. In 1950, while the entrance of the inlet to the gulf was open, strong currents of two miles per hour occasionally flowed through the inlet. At this time the only reduced, unconsolidated bottom type present was in the center of Mud Slough and along the Matagorda shoreline. In November of 1956 about a year after the entrance to the gulf closed the area of reduced, unconsolidated muds considerably enlarged and was found over most of Cedar Bayou.

Vincent's Slough (Figure 5), a small body of water in the washover fan on St. Joseph's Island, is connected during high water to Cedar Bayou and on rare occasions to the gulf.

Recent History of Cedar Bayou

Most of the early history of Cedar Bayou is unknown, but apparently this natural inlet was normally open to the gulf during late historic times until early this century. Several maps from 1836 through 1927 show Cedar Bayou open. Cedar Bayou was reputedly used by Lafitte in the early 1800's (Huson, 1953). The name Tuya Bayou was used for the inlet, but most maps previous to 1900 list an opening (often poorly defined) between Pass Cavallo and Aransas Pass as Espiritu Santo Pass or Inlet. According to Huson (1953) there were plans to block Cedar Bayou in 1856 in order to better maintain ship channels to the south.

Galtsoff (1931) states that water flowed over the bar at the gulf mouth in 1925 during high tide, and the authors have an unconfirmed report that the mouth was open wide in 1924. U.S. Coast and Geodetic Maps show Cedar Bayou open through 1927. Collier and Hedgpeth (1950) stated that Cedar Bayou was closed during Collier's survey in 1936–1938. The Annual Reports of the Texas Game, Fish, and Oyster Commission first mention Cedar Bayou in the 1937–1938 reports, when it was closed. According to later reports it was dredged by the Commission in March through May, 1939 and finally opened in November, 1939 (Annual Reports of the Texas Game, Fish, and Oyster Commission, 1938–39, 1939–40). The latter report states that three miles of the channel had been dredged and water was flowing through the pass.

Since 1939 Cedar Bayou had remained more or less open until 1955, according to Mr. Clyde Townsend, a Rockport sportsman who worked on Matagorda Island during this time. Photographs by the U.S. Naval Air Station of Corpus Christi taken on August 30, 1949 show Cedar Bayou was open to the Gulf of Mexico at the mid-point of the zone of migration[3] (Figure 6). At this time Vincent's Slough was connected to the gulf but not to Cedar Bayou. Vincent's Slough was connected to the gulf in 1942–1944, but not for any length of time after these dates.

[3] The mouth of Cedar Bayou migrates through a well-defined zone (Figures 5 and 6). The ends of this zone are well marked with vegetation. Probably the frequency of washovers which cover this zone keep vegetation from reducing its length. Dry, onshore winds in spring and summer form migrating dunes in the zone, but these are not anchored, and rapidly dissipate.

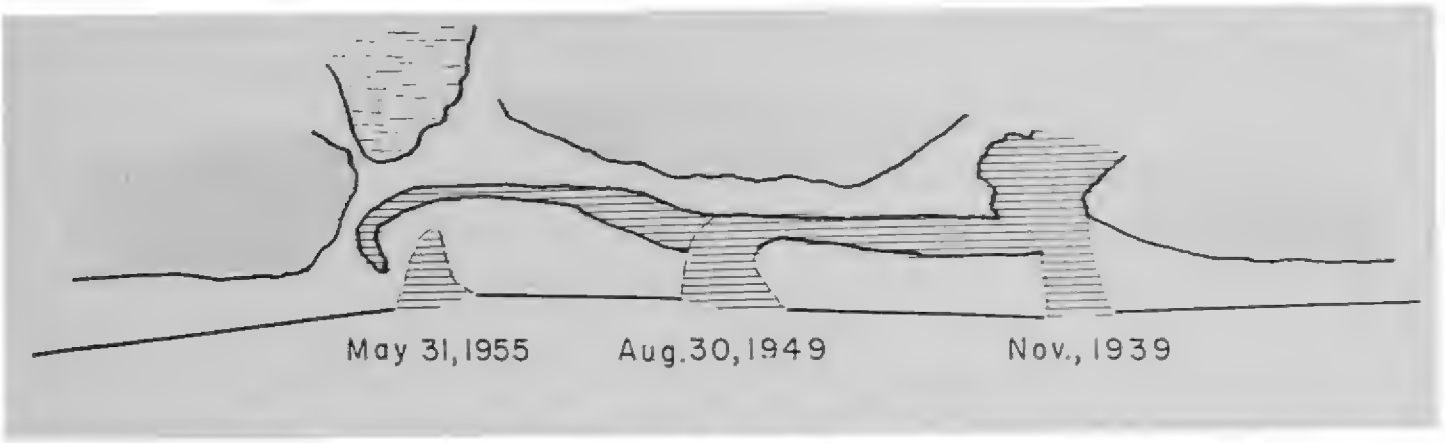

FIG. 6. Diagrammatic view of gulf mouth of Cedar Bayou showing migration from its opening in 1939 to its closing in 1955.

Photographs in the Marine Laboratory files show the gulf mouth of Cedar Bayou as far south as Vincent's Slough (south end of migration zone) on March 31, 1955. A photograph taken in February, 1954 shows the mouth nearly to this point. Photographs taken on May 31, 1955 show the mouth shoaled at this point and not connected to Vincent's Slough. Photographs dated September, 1955 show the inlet connected to the gulf by a small rivulet, but this was only temporary. The final closing may have been from the effects of Hurricane Janet on September 21, but this has not been determined.

Cedar Bayou remained shoaled from this time until November 22, 1956 when through local sportsmen's efforts the mouth was opened with a dragline. By December 17 the mouth had started to erode on the south side and deposit sediment on the north side (Figure 4). The pass remained open at least through February 11, 1957 when the channel shifted to the south and became very shallow. Between this date and March 22, when the area was again visited, it had closed completely and wind-blown sand had obscured all evidence of its being open.

The next apparent opening was during Hurricane Audrey when a rise in gulf tides of over three feet pushed waters over the zone of migration from June 27 through July 1, 1957. These waters did not scour a large channel, but formed several shallow ones. None of these were deep enough to form a permanent inlet. Heavy river discharge pushed small amounts of water into the gulf on September 18, 1957 and again during early January, 1958. Vincent's Slough poured some water into the gulf during the weekend of February 22–23, 1958 during a high northwest wind. Apparently this is not an uncommon happening during the fall and early spring due to high river discharge and coincident north winds.

Another washover occurred on September 5–6, 1958 from high tides of Tropical Storm Ella, but the effects on the area were not studied.

In 1959 Cedar Bayou was redredged and certain changes were made in its features. Mud Slough was completely blocked off by spoil and the new channel was dug through a point of land due west from Grass Island, leaving a second island across from the main channel.

Hydrography

EFFECTS OF RIVER DISCHARGE AND WIND ON THE HYDROGRAPHY OF CEDAR BAYOU

Unfortunately, reliable information on the gulf mouth of Cedar Bayou is available only from 1936 to the present. It was open for roughly 16 years (1939–1955) after it

was dredged. For 15 of those years the Intracoastal Waterway was in its present position. Probably this waterway carried large volumes of water south which influenced Mesquite Bay before 1940.

The transport of water through the inland waterway was observed in the winter and early spring of 1957–1958, when Cedar Bayou was essentially closed. Water hyacinth, *Eichhornia crassipes* (Mart.) Solms, moved south into the area after the floods of early March, 1958. The origin of these water plants is the lower Guadalupe River. No water hyacinths were found in Mesquite Bay but they were not uncommon in the Intracoastal Waterway from San Antonio Bay to Aransas Bay as far south as Rockport. According to Mr. Floyd Brown, who has fished the area for many years, water hyacinths normally came into Mesquite Bay during floods when the pass was open also but they did not reach Aransas Bay.

Mesquite Bay and the discharge through the pass are largely under the influence of the Guadalupe River System (Collier and Hedgpeth, 1950; Parker, 1955) (Figure 7). Average river discharge for this system from 1940 to 1949 was 1,972 cfs. During this time the mouth migrated approximately one-half of the distance across its total migration zone (Figure 6). From 1950–1955, when the mouth finally shoaled, river discharge averaged 744 cfs, or less than half the former figure. This reduction in river discharge is further emphasized in Figure 8. The pass mouth migrated an equal distance in half the time with half the river discharge. Again when the mouth was opened in 1956, river discharge was extremely low (less than 500 cfs) and the mouth rapidly shoaled.

Other factors affect pass discharge. Some of the increased migration in later years may have been due to slowed current velocities rounding the bend of the mouth (Figure 6). Price (1952) and Lohse (1955) have emphasized the importance of north winds in moving water masses. Collier and Hedgpeth (1950) said that tides in Texas bays are often confused by winds. Barlow (1956) found that salinity in Great Pond, Massachusetts was largely determined by day-to-day changes in wind direction and magnitude rather than by tides or fresh-water supply. It was observed in 1957 and 1958 that north winds moved great volumes of water into and through Mesquite Bay. When these winds are blowing, water levels raise at stations 3 and 14 and drop near station 6, suggesting

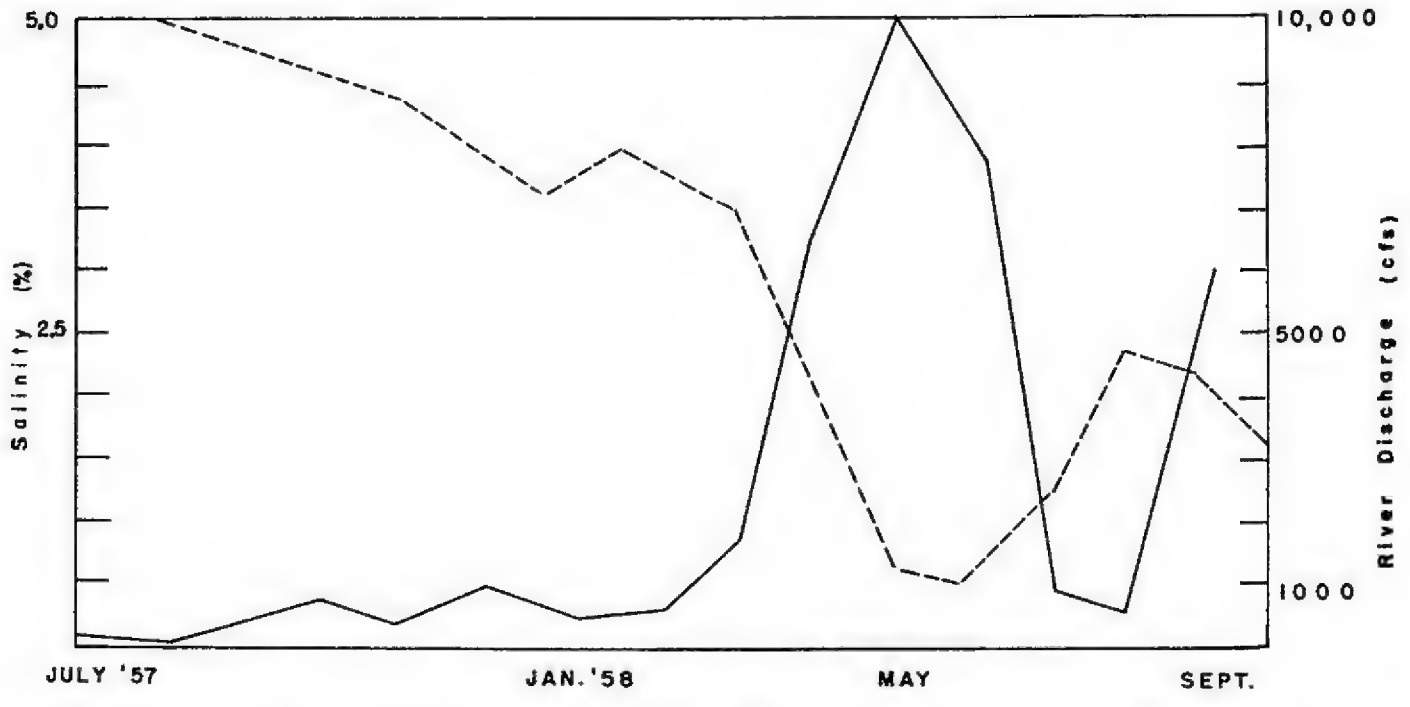

FIG. 7. Correlation of average monthly Mesquite Bay salinity in per cent (dashed and dotted line) with average monthly river discharge (solid line).

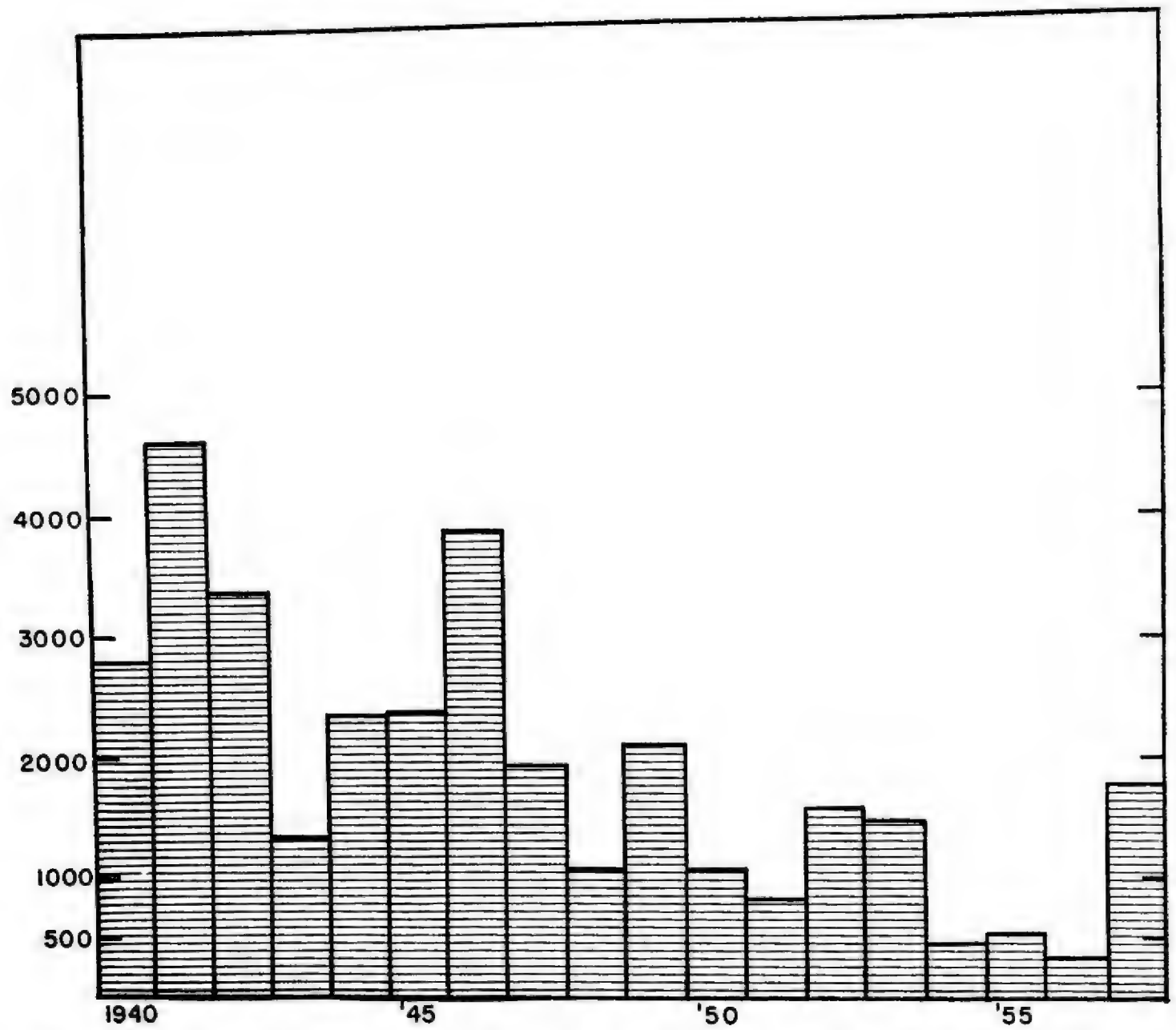

FIG. 8. Average yearly river discharge for the Guadalupe River System from 1940 through 1957 (September) in cfs (cubic feet per second flow).

movement similar to a seiche. Simmons (1957) has shown that seiches occur in the Laguna Madre and they are probably common in all Texas bays.

The effects of north winds may be inferred from salinity data gained during the 1957–1958 study. In summer months when onshore winds predominated and river discharge was small, water movement was small. The salinity distribution of Mesquite Bay during such a condition is shown in Figure 9.

During strong northers and high river discharge, water movements are more extreme. On the morning of February 11, 1958 a 15 mph northeast wind prevailed on the Central Texas Coast. The salinity distribution of Mesquite Bay is presented in Figure 10. The isohalines show a direct movement toward the south-southwest. Water levels were rising at this time due to the flooding of the Guadalupe River System. Salinity values obtained in the Intracoastal Waterway north of Mesquite Bay and in San Antonio Bay indicated that this mass of fresh water was pushing against Mesquite Bay waters and turning toward a course of lesser resistance, the Intracoastal Waterway, presumably to be flushed out at Aransas Pass. Salinities in the waterway as far south as Aransas Bay were 1.9 ppt.

On February 27, 1958 a 30–33 mph northwest wind prevailed. The salinity distribution of Mesquite Bay is shown in Figure 11. This intrusion of fresher water extends farther than when winds are less in force, as illustrated in Figure 10.

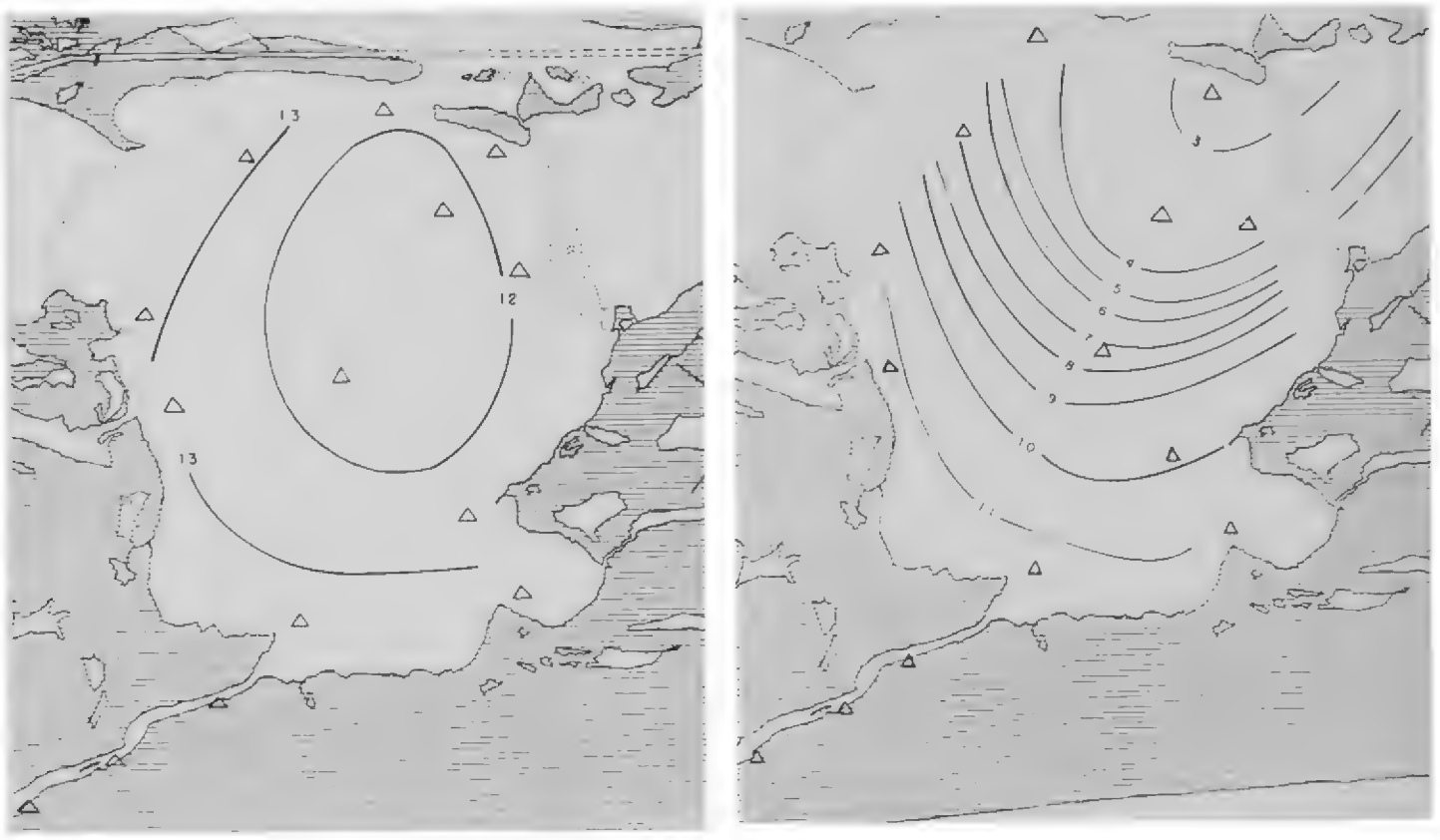

FIG. 9. Generalized isohalines, July 17, 1957, during negligible river discharge and no wind. Triangles represent salinity stations.

FIG. 10. Generalized isohalines, February 11, 1958, during high river discharge and a 15 mile per hour northeast wind. Triangles represent salinity stations.

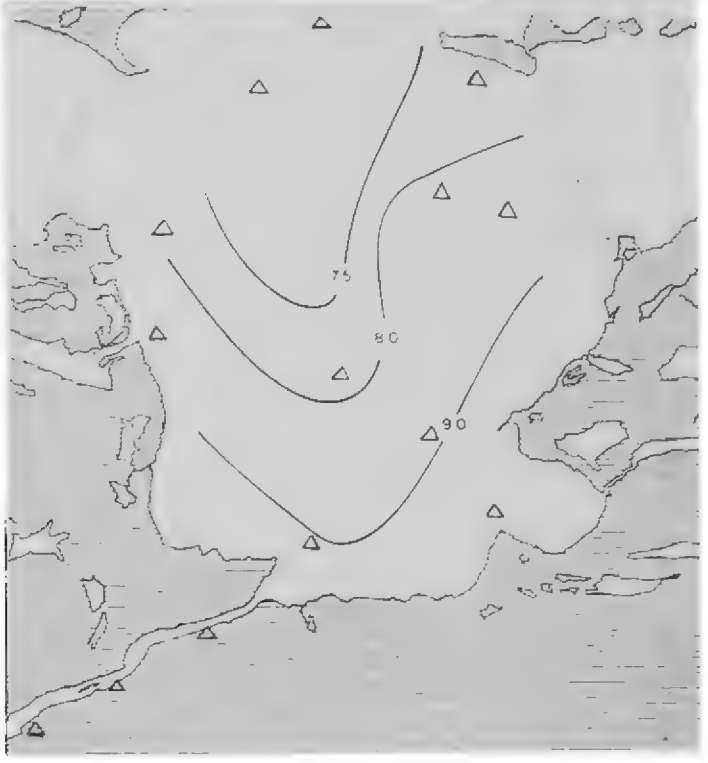

FIG. 11. Generalized isohalines, February 27, 1958, during high river discharge and a 30–33 mile per hour northwest wind. Triangles represent salinity stations.

North winds apparently move water masses great distances. Shepard and Moore (1955) claim that some of the sediment of San Antonio Bay is derived from the north through Espiritu Santo Bay during northers. On January 3, 1958 the average salinity of Mesquite Bay was 7.0 ppt. For the next three days high north winds with velocities over 30 mph prevailed on the Central Texas Coast. By January 8 the average salinity was

17.1 ppt a rise of 10.1 ppt. Winds apparently drove waters from Espiritu Santo Bay, which normally has relatively high salinity, to Mesquite Bay. T. R. Leary (personal communication) found the converse in middle Aransas Bay where salinities dropped suddenly after the norther. From these data it seems that Mesquite Bay waters were blown about 20 miles south or an average of nearly seven miles per day.

During periods of north winds and high discharge, southerly currents are very apparent in the Intracoastal Waterway from San Antonio to Aransas Bays. Rough measurements with fluorescein indicate that these currents may be three or four times as great as currents near Ayres Dugout. It seems that this segment of the waterway is a distinct hydrographic unit, somewhat analogous to a river.

Cedar Bayou closed during dry years. Analyses of weather maps were started to determine if there were differences in wind systems between dry and wet years. The analyses are not complete, but there seems to be little evidence that there was any large reduction in northerly winds during the drought.

The closure of Cedar Bayou at the gulf mouth seems to be due mainly to reduced river discharge resulting in less tidal flushing. Cedar Bayou closed in 1955 when Mesquite Bay was essentially a negative estuary and it closed previously around 1930. River discharge figures are not available during this time, but there was also a drought in the early 1930's (Price and Gunter, 1942). Johnson (1919) attributed the presence of inlets remote from streams to the absence of alongshore currents, thereby indicating river discharge is important to inlet maintenance.

The long axis of Cedar Bayou lying NNE-SSW indicates that northerly winds have been important in its formation and maintenance. Blankenship (1953) pointed out that Cedar Bayou was a more successful washover channel than Vincent's Slough, and this is undoubtedly due to its orientation. Vincent's Slough is rarely connected with the gulf, and when the whole zone of migration is shoaled more washovers occur from Cedar Bayou than from Vincent's Slough.

The migration of Cedar Bayou appears to be regulated by three opposed factors: (1) longshore current providing a net southeasterly movement by depositing sediment on the north side of the inlet mouth; (2) river discharge pushing water out the mouth, retarding migration by erosion; (3) north winds providing an acceleration of ebbing tides. It must be noted here, however, that neither the heavy floods or northers of 1935 and 1957 provided the energy to open Cedar Bayou.

Effects of Cedar Bayou on the Hydrography of Mesquite Bay

Knowledge of an influence of gulf waters on the hydrography of Cedar Bayou and Mesquite Bay is necessary for the interpretation of the possible biological effects of opening Cedar Bayou. Salinities for Mesquite Bay are not available during a wet year with Cedar Bayou open. Some salinity data was obtained by Parker (1959) during the drought years and by one of us in 1950–1951 and after the mouth was opened in 1956 (Table 1).

Salinity and temperature records were maintained throughout the 1950–1951 study. Table 2 is the record of salinity and water temperature at the gulf entrance to Cedar Bayou, at Grass Island, and in Mesquite Bay near the entrance to Cedar Bayou.

It appears that, in many cases, gulf water extends all the way through the inlet and that, in other cases, bay water fills the inlet (April, May, and July, 1950; and parts of February and March, 1950). In other instances (October and December, 1949; Jan-

TABLE 1

Salinity and temperature in Mesquite Bay in 1956 with Cedar Bayou closed and in 1957 with Cedar Bayou open

Date	Station	Salinity ppt	Temperature° C
November 9, 1956	1	44.5	15.4
	10	44.5	15.1
	3	45.3	15.0
	2	.....	14.7
January 29, 1957	1	36.6	13.9
	10	38.0	13.5
	3	38.6	14.4
(Gulf tide low)	12	35.8	15.4
	13	35.3	15.1
	14	36.6	15.1
	4	37.6	15.1
	5	37.8	14.4
	8	37.5	14.9
	7	37.9	14.6
	6	36.8	14.8
	11	38.0	15.5
February 11, 1957	1	40.1	22.3
	2	38.5	22.4
(Gulf tide high)	3	38.5	23.0
	12	34.4	23.5
	13	34.2	23.5
	14	33.6	21.9
	7	38.8	24.0
	6	40.6	24.1
March 22, 1957	1	34.6	21.2
	10	35.7	21.3
	3	35.9	21.0
	12	36.8	21.2
	13	38.5	21.4
	14	33.8	.....
	4	36.0	22.8

uary and February, 1950) there was a definite demarcation between water in the gulf and in the bay. In a few cases (September, 1949, January, 1950, and March, 1950), sections of bay or gulf water appeared to have been broken off and sandwiched between higher or lower salinity water. These cases usually occurred during periods of abroupt north winds resulting in rapidly changing current flow.

As a further check on the movement of water through the inlet, samples were obtained at one station at intervals throughout two complete tidal changes. These data were given by Parker (1955) and indicated that the water mass entered the inlet from the gulf and receded virtually intact.

It must be noted, however, that during flood tides and heavy northers, the normal ebb and flow of tide was altered. In some cases water flowed into the bay for five or more days without ebbing, and a similarly sustained outflow occured in winter during high north winds.

High water of Hurricane Audrey caused a flow of gulf water into the bay. Tidal waters flowed over the islands into Cedar Bayou and Mesquite Bay from June 27 to July 1, 1957. Salinities in Mesquite Bay increased from less than 2 ppt to 12 ppt from this intrusion of gulf water. Since the salinity of gulf water that entered was about 22 ppt, an estimated volume of water equal to the initial volume of Mesquite Bay or something over one billion cubic feet of gulf water entered during the washover.

A spreading wedge of saltier water from this intrusion was first recorded on June 27 and again on July 1 along the north shore of the bay, but not in the center. Unfortu-

nately, no data were taken for the south shore of the bay during the washover. A sharp interface was evident near station three where highly turbid gulf water (light transmission, 77.8 per cent) of a salinity of 21 ppt met fresher, clearer water (5.2 ppt, 85.2 per cent). The water samples were taken six feet apart on either side of the line marking the boundary between the two water masses. This interface was sharp only at the surface. Bottom salinities and turbidities through the area showed gradual mixing. This

TABLE 2

Salinity and temperature at selected points in or near Cedar Bayou with the pass open

Date	Location	Salinity ppt	Water temperature°C
Sept., 1949	Gulf entrance	33.5	.....
	Grass island	20.0	.....
	Bay entrance	33.0	.....
Oct., 1949	Gulf	29.9	26.9
	Grass island	29.5	27.1
	Bay entrance	26.9	28.1
Nov., 1949	Gulf entrance	23.6	18.1
	Bay entrance	22.5	18.1
Dec., 1949	Gulf entrance	31.1	22.4
	Grass island	22.7	22.1
	Bay entrance	21.1	22.7
Jan., 1950			
Week 1	Gulf entrance	27.9	18.8
Week 1	Grass island	31.0	18.8
Week 1	Bay entrance	28.2	19.6
Week 2	Gulf entrance	28.5	20.4
Week 2	Grass island	28.3	20.4
Week 2	Bay entrance	28.1	20.6
Week 3	Gulf entrance	28.4	20.4
Week 3	Bay entrance	24.9	.....
March, 1950			
Week 1	Gulf entrance	24.1	17.5
Week 1	Bay entrance	22.9	19.0
Week 2			
Week 2	Gulf entrance	24.1	16.8
Week 2	Grass island	23.8	18.6
Week 2	Bay entrance	23.8	19.0
Week 3	Gulf entrance	20.1	20.3
Week 3	Grass island	26.4	21.3
Week 3	Bay entrance	25.8	21.3
Week 4	Gulf entrance	27.6	21.6
Week 4	Bay entrance	25.9	21.5
April, 1950			
Week 2	Gulf entrance	26.0	23.4
Week 2	Bay entrance	26.3	24.7
Week 3	Gulf entrance	26.3	24.1
Week 3	Bay entrance	26.2	24.5
May, 1950	Gulf entrance	25.1	.....
	Grass island	25.4	27.6
	Bay entrance	25.3	27.9
	Gulf entrance	24.1	. ...
	Grass island	24.2	28.1
	Bay entrance	24.2	28.3
	Gulf entrance	.....	.....
	Grass island	26.2	29.0
	Bay entrance	26.2	29.0
	Gulf entrance	25.3	27.2
	Bay entrance	25.4	27.7
	Gulf entrance	23.7	28.2
	Bay entrance	24.2	28.2
	Gulf entrance	26.3	29.1
	Bay entrance	26.2	28.6
July, 1950	Gulf entrance	36.9	30.0
	Grass island	36.9	29.6
	Bay entrance	.....	.....

interface was maintained through July 1, when the highly turbid surface water was still in approximately the same position, but the salinity of the gulf water was slightly lower (20.0 ppt) and that of the fresher water slightly higher (7.2 ppt). Shortly after this time the inflow of gulf water stopped, and apparently there was little return flow through Cedar Bayou.

Fish Trap Study in the Open Pass in 1950–1951

The fish traps were in at least partial operation from January 23, 1950 to July 10, 1951. The actual number of hours of operation was 5,995. Sometimes when one trap was out of operation, trammel nets were stretched across the inlet and numerous fish were captured.

During the period the traps were in operation, 281,948 fish were captured. Over 240,000 or 85 per cent of these were going from the bays to the gulf. Most movement was nocturnal (Figures 12 and 13) with about 89 per cent of the outward and 70 per cent of the inward migration at night. The 90 species of fish collected are listed in mimeographed reports (Simmons, 1950 and 1951), and the numbers of major species are listed in Table 3. The total number of fishes taken by month, time of day, and direction is graphed in Figures 12 and 13.

Over 75,000 blue crabs were captured and literally millions of penaeid shrimp migrated through the inlet.

Major Migrations

Cynoscion nebulosus (Figure 14): In 1950 spotted sea trout, *Cynoscion nebulosus*, entered Cedar Bayou in late March. From May until late June there was a definite bayward movement. Many of these trout were ripe and some of these which were tagged were later recovered in secondary bays in a spent condition.[4] During May and June, however, there were more male trout than females. Of the 50 trout moving inward in May, 35 were males. In June, 72 fish were taken in the trap moving to the bay and 45

Table 3

Major species taken in fish traps, 1950–1951

Species	Number taken
Micropogon undulatus	198,352
Galeichthys felis	29,107
Citharichthys spilopterus	9,700
Cynoscion arenarius	7,072
Bairdiella chrysura	6,373
Lagodon rhomboides	5,122
Eucinostomus spp.	2,947
Trichiurus lepturus	1,500
Brevoortia sp.	1,700
Cynoscion nebulosus	684
*Paralichthys spp.**	819
Sciaenops ocellata	136
Pogonias cromis	42
**P. lethostigma and albigutla*	

[4] While Cedar Bayou was closed in 1958, *C. nebulosus* apparently spawned in the bay, as sexually mature males and females were abundant in April and May. Young-of-year were taken in trawls in all months except February. Miles (1951) did not note spawning activity in Mesquite Bay, but his work was centered in Copano Bay.

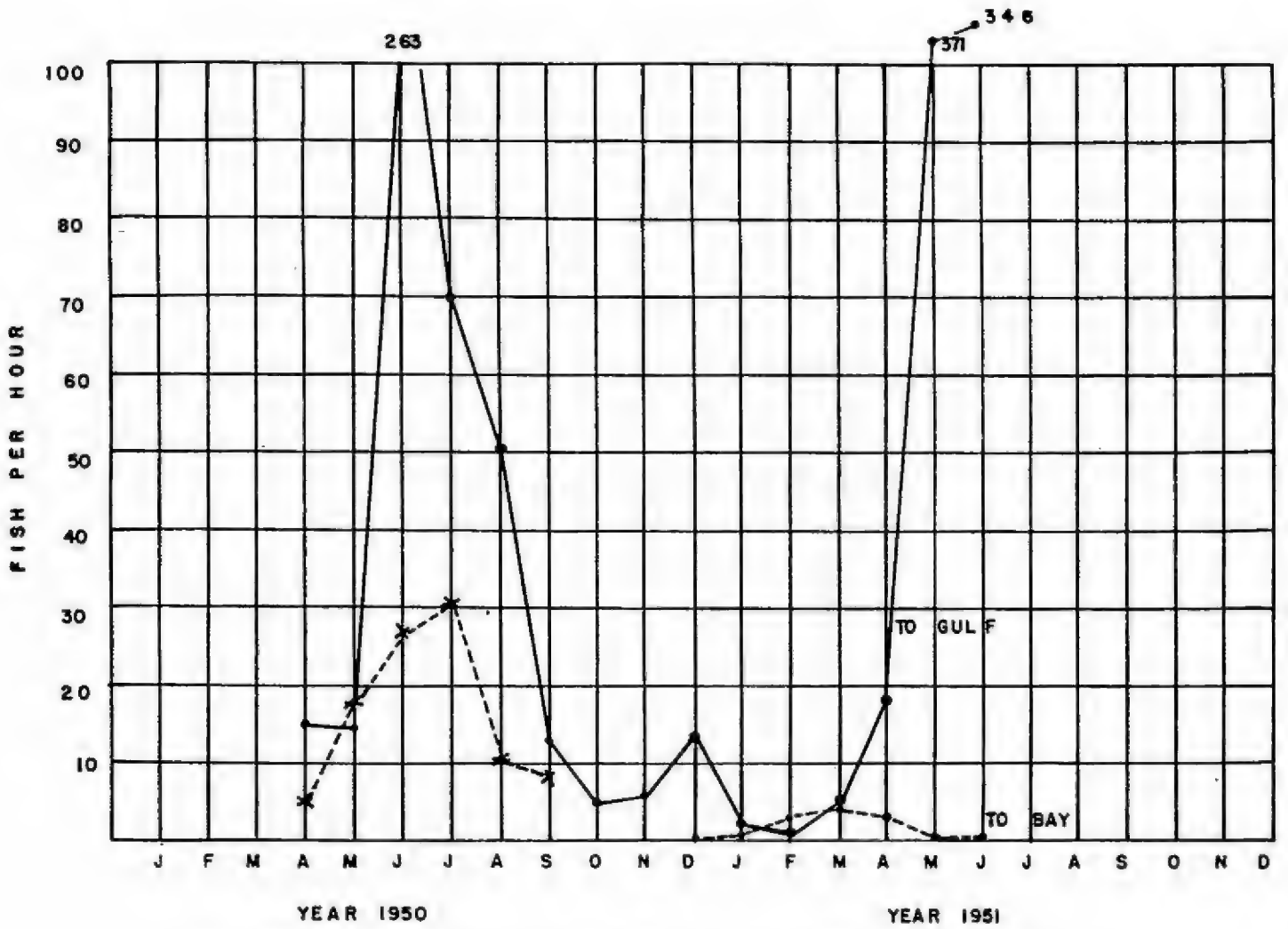

FIG. 12. Nocturnal movement of fish from bay to gulf and from gulf to bay.

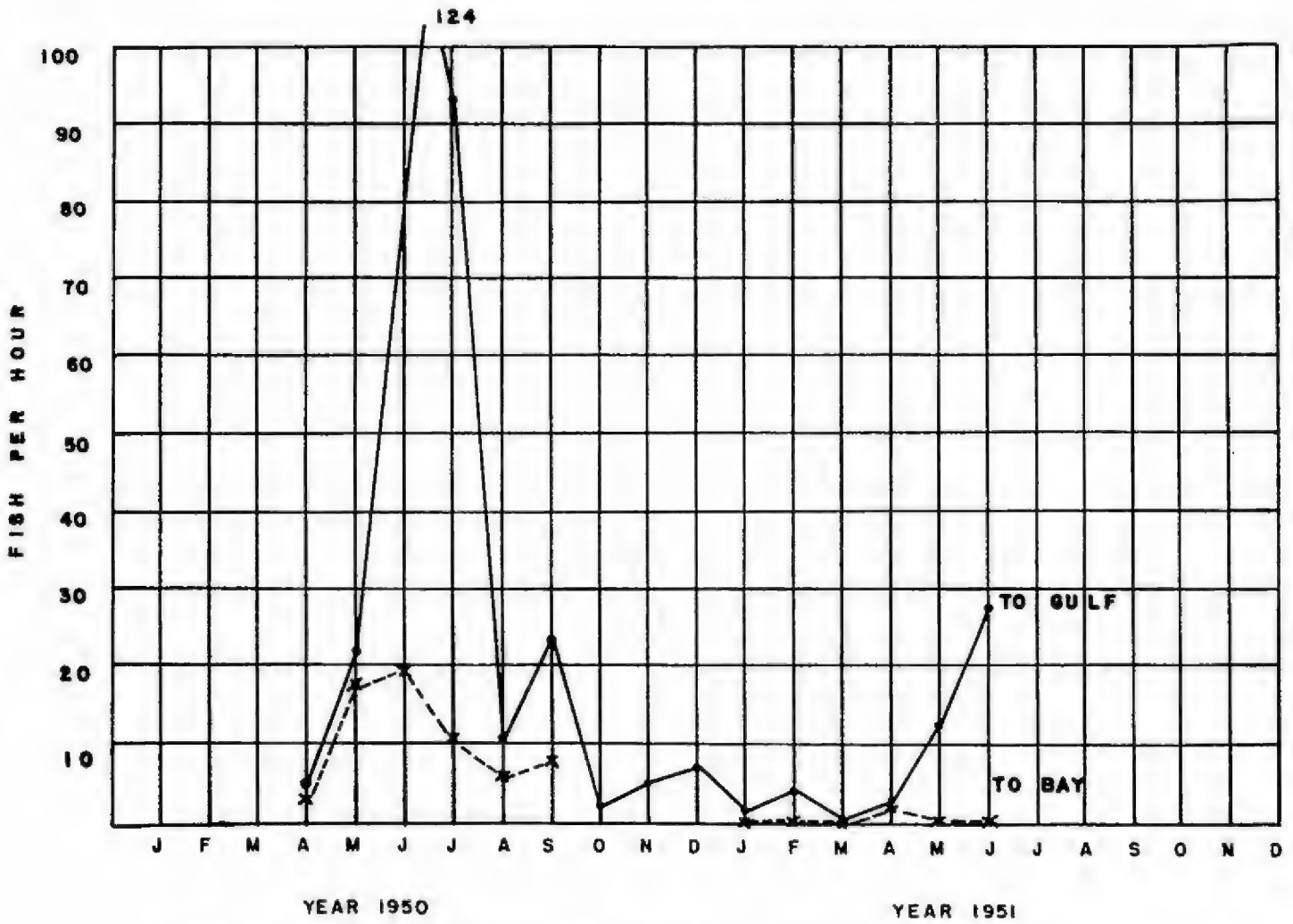

FIG. 13. Diurnal movement of fish from bay to gulf and from gulf to bay.

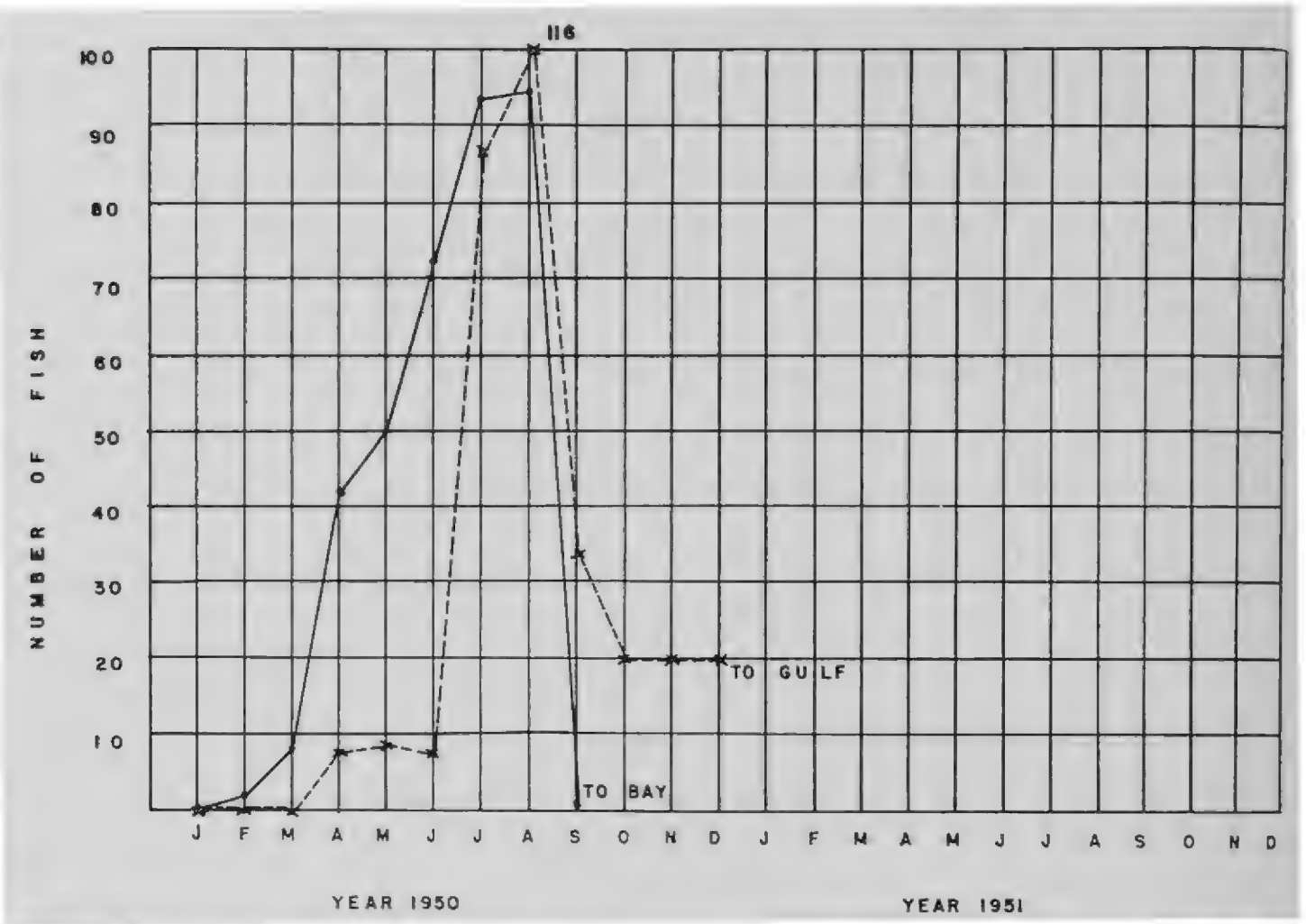

FIG. 14. Gulfward and bayward seasonal movement of sea trout, *Cynoscion nebulosus*, through Cedar Bayou.

of these were males. In July, 180 trout were captured, and in August this number increased to 210. During these two months there was little evidence of a regular migratory pattern and it was not always possible to determine sexual condition. In September 34 trout were taken moving to the gulf. This number declined to 20 in October, November, and December. In each case movement was gulfward, and in November and December fish were caught only when sudden drops in water temperature occurred. Few were taken in the traps in January, February, or March and only 50 were captured moving to the bays in April.

Most trout captured in the traps ranged in size from 170 to 300 mm; the smallest trout taken measured 160 mm, the largest 550 mm. Length-frequency data from the trap catch are shown graphically in Figure 15.

In many instances trout were captured in gill nets and trammel nets. Using these data together with those from the traps it is possible to indicate the age groups as determined by Miles (1951). Most trout in Cedar Bayou during spring months were two years old or less, but these were displaced by larger fish as the season progressed. The presence of larger-size fish in April, 1951 was probably due to the heavy fish mortality in the bays during a January freeze which was described by Gunter and Hildebrand (1951). Many fish in the bay perished while those in the gulf were little affected. In April these fish were from the gulf. On April 20, 1951, hundreds were found near the gulf entrance to the inlet. These did not enter far into Cedar Bayou but passed outward again. Studies in the Laguna Madre by Simmons (1957) indicated that many trout never leave the bays. Also, it is possible that others remain in the gulf most of the year and that the classic picture of inward spring migration and outward fall migration might have to be modified. It was noted in Cedar Bayou that trout did not pass through the inlet until water

temperature reached 19–20° C and Simmons (1957) found that these fish were not greatly affected by changes in salinity from 30 ppt to 50 ppt. It appears that water temperature and tidal flow affects movements more than changes in salinity.

Sciaenops ocellatus: Channel Bass (Redfish), *Sciaenops ocellatus*, were difficult to capture in traps of the type used in the 1950–1951 study. However, enough were captured to give some information on migratory patterns. Many fish, ranging in size from 400 to 775 mm. were observed feeding at the mouth of Cedar Bayou in April of each year. These fish did not enter far into the bayou. On April 20, 1951, trammel nets captured 134 of these fish. These were then tagged and released. Thirty were later recaptured, all in the gulf. Recovery points ranged from 10 miles south of Port Aransas to 10 miles north of Pass Cavallo. The first author, in 1948, observed a school of redfish much larger than any ever found in the bay in the Gulf of Mexico 12 miles off Sabine Pass. Many individuals passed near the vessel and all were at least 90 cm in length. A few individuals were probably 150 cm long. Redfish near this size were never captured in the traps. However, Miles (1951), Breuer (1957), and Simmons (1957) reported large redfish in the bays prior to spawning and a few after spawning. Therefore, some large redfish utilize inlets but inlets other than Cedar Bayou are apparently preferred. In both summers of the study many small redfish were found moving bayward through the inlet but whether this was a real migration or a simple feeding movement is not known. It appears that Cedar Bayou was utilized by small redfish and some of the spawning stock but that large individuals remained in the gulf after they reached sexual maturity.

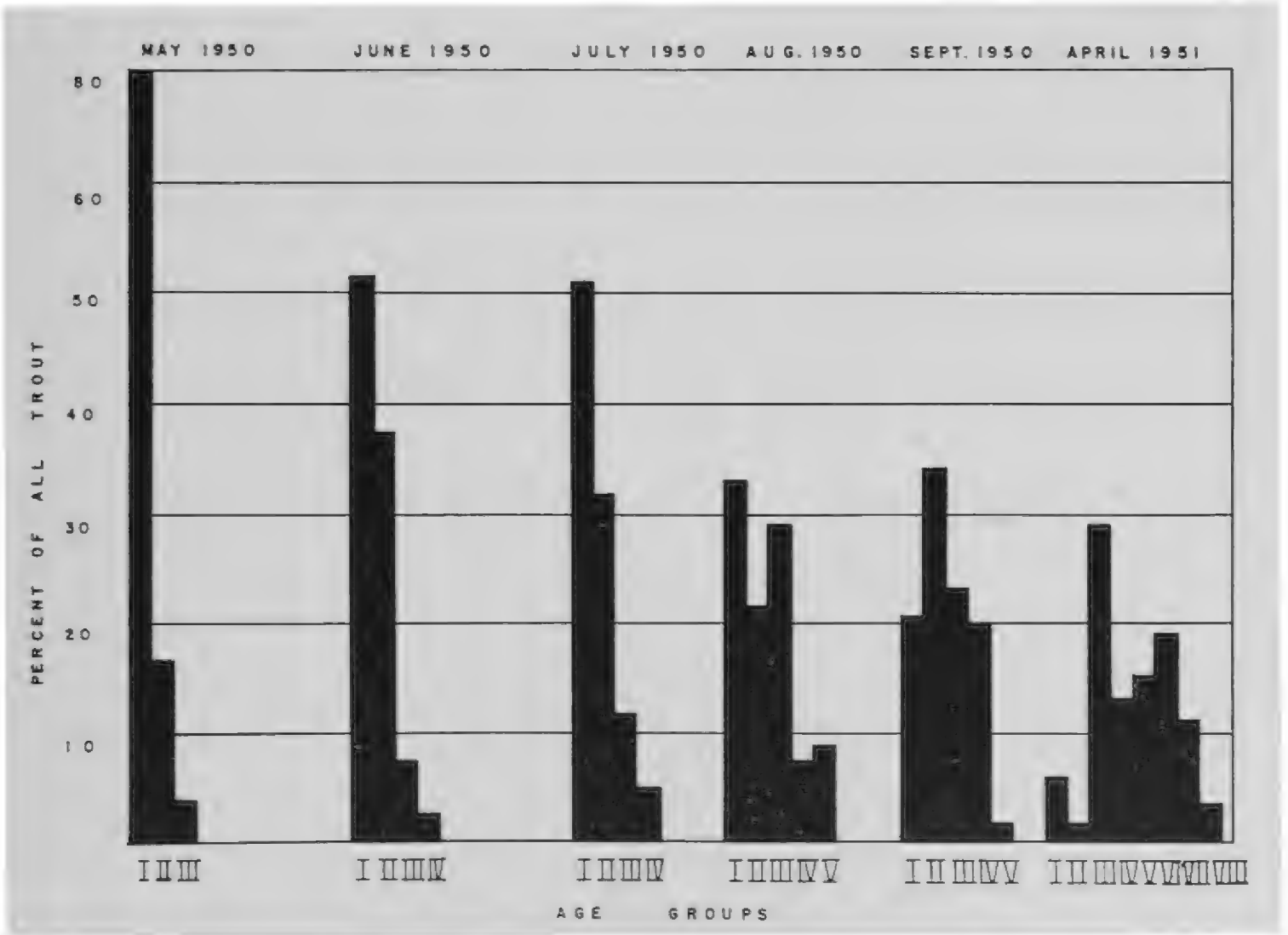

FIG. 15. Age groups of sea trout, *Cynoscion nebulosus*, in Cedar Bayou by months in 1950–1951.

Paralichthys lethostigma (Figure 16) : Southern flounder, *Paralichthys lethostigma,* and gulf flounder, *P. albigutta,* definitely utilized Cedar Bayou as a migratory route. All of the larger specimens examined were southern flounder, but some of the post larval specimens appeared to be gulf flounder. For the purpose of this paper all were summed as southern flounder. In April and May, 1950, movement seemed to be random. Of the 29 fish captured during this period 18 were moving toward the bay and 11 toward the gulf. There were 19 males ranging in size from 225–360 mm, one female in this size bracket, three females larger than 375 mm, and six fish under 200 mm.

In June, 1950, 43 were captured, and 38 of these were moving toward the bay. In July there was a sharp increase in the number of fish as 141 were captured in traps or nets. Movement appeared to be radom as it was in August when 98 fish were taken.

In September, 1950, 171 flounder were captured and 125 of these were moving gulfward. In November and December movement was gulfward and 276 fish were captured. Some of these were taken by gigs but all movements recorded by traps was outward. In November all 85 fish taken by gigs were males ranging in size from 150–300 mm. In December all 236 fish were females ranging in size from 300–520 mm. Tagged fish from the trap were later recaptured by shrimp boats operating in the gulf in waters 20 fathoms deep.

No flounder were found in January or February, 1951 but in April, 1951, young flounder moved from the gulf to the bay. Traps captured 54 of these ranging in size from 25–54 mm and many more were observed in shallow water near Grass Island. None were found in May, 1951 when larger flounder again appeared in the inlet, but

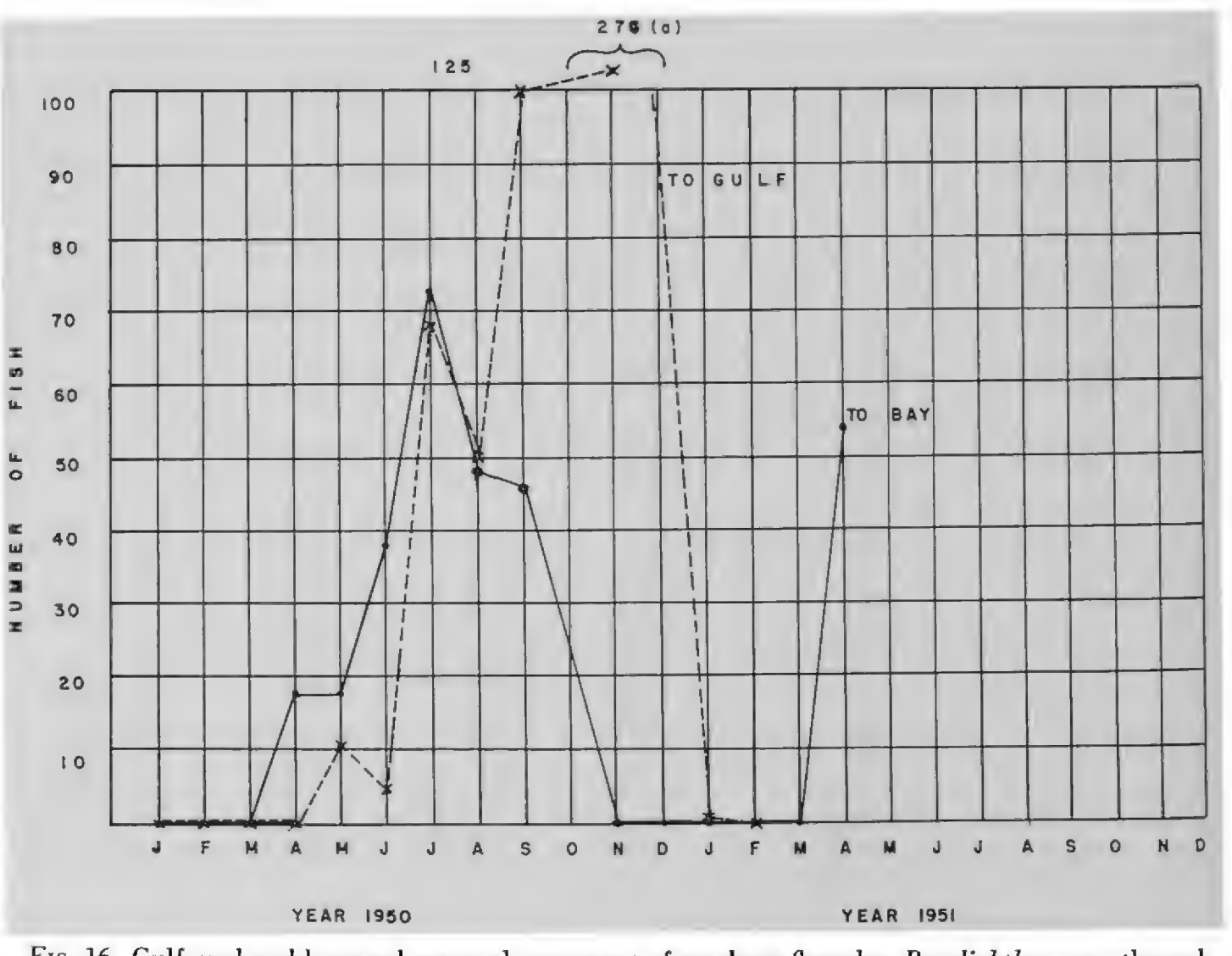

FIG. 16. Gulfward and bayward seasonal movement of southern flounder, *Paralichthys spp.*, through Cedar Bayou.

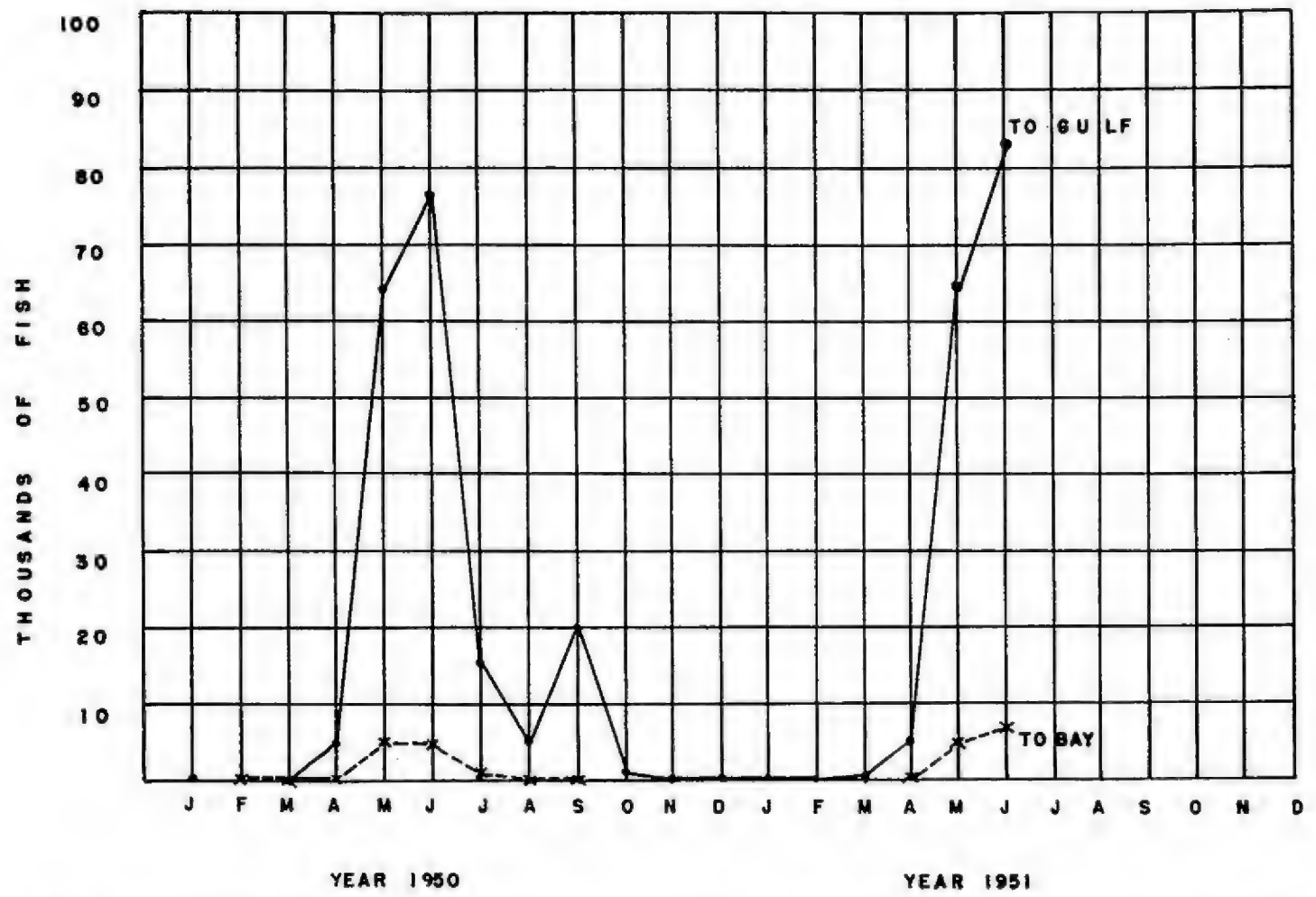

FIG. 17. Gulfward and bayward seasonal movement of *Micropogon undulatus* and *Leiostomus xanthurus* through Cedar Bayou.

scattered individuals of the 0 year class were found in June and July[5]. The outward movement in the fall was accentuated by drops in water temperature and the inward movement in the spring by incoming tides. It is apparent from the records of Miles (1951), Breuer (1957), and Simmons (1957) that some flounder may be found in the bays at all seasons of the year. Fish tagged in the bay were often recaptured in the same spot several months later. Mr. Robert Kemp, former biologist of the Texas Game and Fish Commission (personal communication), reported finding flounder in freshwater lakes in 1959. These fish ranged in size from three to seven pounds and were gravid. However, in spite of these known exceptions, the observations in Cedar Bayou and the heavy fishing pressure near Port Aransas in the fall of the year show that many flounder pass through inlets (Springer and Pirson, 1958). Figure 17 shows the seasonal movements of flounder in Cedar Bayou.

Micropogon and *Leiostomus* (Figure 17): Croakers, *Micropogon undulatus*, and sport, *Leiostomus xanthurus*, were also extensively taken in Cedar Bayou. Gunter (1945a) found *M. undulatus* to be the most numerous fish in the bay and it was also the most numerous fish passing through the inlet. In May, 1951, 64,042 moved toward the gulf; in June this number increased to 76,116. In September, 1950 about 20,000 larger croakers were taken as they moved toward the gulf. In contrast to the fish taken in summer, which were all less than 176 mm long, those captured in September were over 225 mm long and many were gravid. Pearson (1929) reported that croakers spawn in the gulf, probably near passes. Thousands of port-larval croakers 10–25 mm long were found in Cedar Bayou on incoming tides in October and November, 1950. However,

[5] Young *P. lethostigma* (37–120 mm) were abundant in Cedar Bayou in March through May, 1958. Larger individuals were more common in the summer of 1957.

the cause for the intense outward migration during the summer (Figure 17) is not understood.

Cynoscion arenarius: About 3,000 mature sand trout, *Cynoscion arenarius,* were captured in May, 1950, as they moved through the inlet from the bay to the gulf. In June of each year of the study post-larval fish were captured with push-nets as they moved bayward on incoming tides. Apparently the habits of the sand trout and the spotted sea trout are different.

Other fishes found to utilize the inlet in migration were catfish, cutlass fish, mojarras, drum, silver perch, whiffs, tongue fish, and pigfish. More stingrays than sharks were taken.

Callinectes sapidus (Figure 18): Invertebrates also passed through Cedar Bayou extensively in 1950–1951. The blue crab, *Callinectes sapidus* Rathbun, was a migrant through Cedar Bayou in all months except December, January, and early February. Major movements as indicated by trap records, are indicated in Figure 18.

The main migration began in April when numbers of sponge crabs moved from bay to gulf areas. In May and June the total number increased but this was due almost entirely to migrations of fertilized females as determined by Daugherty (1952). During early June many mature females, sponge crabs, immature females and males went out. The number declined steadily after that time. An inward migration of spent females began in April, reached a peak in July and August, and then declined in September and October. Few crabs were taken after that time.

During February and March millions of larval crabs moved into the bays through

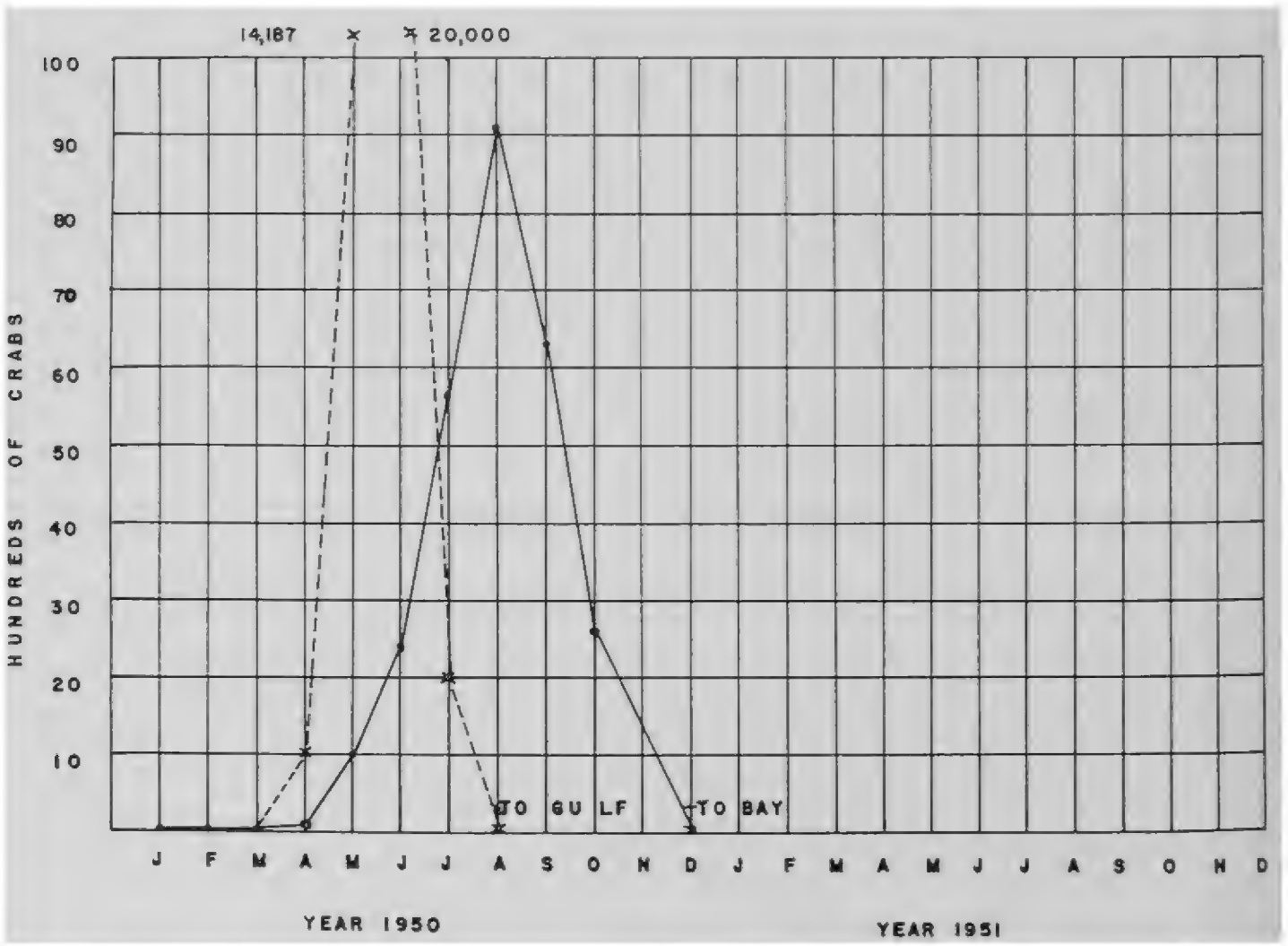

FIG. 18. Gulfward and bayward seasonal movement of blue crab, *Callinectes sapidus*, through Cedar Bayou.

Cedar Bayou. Crabs of very small size appeared in Mesquite Bay during these months in 1957 and 1958. There was no evidence that they had been spawned in the area. It is not easily understood why post-larval crabs did not appear in the inlet in May, June, July, and August when spawning occurred in the gulf.

Penaeus spp.: Of at least equal importance was the movement of commercial shrimp, *Penaeus spp.* through this tidal inlet. It was impossible to determine the actual number which passed through Cedar Bayou as most went through the fences of the trap boxes. On the night of June 14, 1950, however, over 500 pounds were captured as they moved to the gulf. These ranged in size from 80–140 mm and 95 per cent were grooved shrimp, *P. aztecus* and *P. duorarum*. In the period from April until November shrimp of all sizes moved to the gulf, with particularly heavy movement in June and September. All movement was nocturnal. On several occasions these invertebrates were observed to be so densely packed in the water as to reduce visibility to a few inches. By morning no shrimp could be seen in the water but many were found buried in the bottom. The migration in each instance began the following night, by actual observation.

Again in late February and early March the water was cloudy with larval and post-larval shrimp coming in from the gulf, always on incoming tides but independent of nocturnal or diurnal regulation. Post-larval penaeid shrimp were scarce in Mesquite Bay in 1958. A few were taken in plankton nets in April and May. The bay was flushing rapidly at this time; young blue crabs and several post-larval fishes were abundant.

Fish Studies During the Period of Pass Closure in 1957-1958

Studies from June, 1957 through May 1958 were undertaken for comparison with similar studies with Cedar Bayou open. For quantitative study a total of 36 trawl collections were made in Cedar Bayou and 132 in Mesquite Bay. The total number of fish caught and the average number of fish per collection are shown in Table 4.

One species of hermit crab, *Pagurus floridanus*, was found only in Cedar Bayou but another, *Clibinarius vittatus*, was abundant in both bay and bayou.

Two fishes (*Archosargus probatocephalus* and *Gobionellus boleosoma*) were found only in vegetated areas in Cedar Bayou and on oyster reefs.

TABLE 4

Numbers of fishes taken in Cedar Bayou and Mesquite Bay, 1957–1958

Species	Mesquite Bay		Cedar Bayou	
	Total	Average per collection	Total	Average per collection
Bagre marina	160	1.40	1	.02
Galeichthys felis	259	2.10	46	1.20
Bairdiella chrysura	55	.49	3	.....
Leiostomus xanthurus	886	6.70	434	12.00
Micropogon undulatus	3,332	25.90	692	19.20
Stellifer lanceolatus	1	.....	17	.47
Orthopristis chrysopterus	109	.83	4	.11
Citharichthys spilopterus	35	.28	63	1.80
Etropus crossotus	15	.11	37	1.03
Paralichthys lethostigma	38	.28	105	2.90
Gobionellus hastatus	1	.....	26	.72
Sphoeroides nephelus	169	1.29	14	.39
All Fishes	4,541	34.40	1,721	47.80

Seasonal variations in populations of fishes and larger invertebrates were similar to those Gunter (1945a, 1950a) found in Copano Bay. In most species there was a progressive immigration until a peak of population abundance was reached and then a subsequent progressive emigration. The first date of occurrence of a species in early spring was later than in a bay with closer access to the Gulf of Mexico, such as Aransas Bay. This phenomenon is apparently a function of distance. A bay with direct connection with the gulf is a primary bay; other bays are secondary.

For example, the first capture of the new spawn of the most abundant fish taken, *Micropogon undulatus,* was January 8, 1958, when five specimens from 20 to 44 mm were taken. This same species appeared in Cedar Bayou 60 days earlier in 1950 when the pass was open. Breuer (1958) found that many species appeared as much as 60 days earlier in the Lower Laguna Madre after a pass was opened through Padre Island. This delay was also observed in the Upper Laguna Madre in December, 1958 and December, 1959. Pearson (1929) found post-larval *Sciaenops ocellata* near Corpus Christi Pass in mid October and traced these fish until they reached secondary bays several weeks later. Simmons (1957) noted that young redfish appeared in the Upper Laguna Madre in late February and early March.

Even though the observations cited were from other bays and in different years, the fact that the immigration occurred at a later date in these bays for at least six years indicates that a delay might be expected in Mesquite Bay when the pass is closed. Therefore, it is probable that Mesquite Bay, with Cedar Bayou closed, is essentially a secondary bay and with the pass open is a primary bay.

Not all species were entirely absent from Mesquite Bay in winter. Occasionally young-of-year of *Archosargus probatocephalus* and *Cynoscion nebulosus* were captured. Most of the cyprinodonts and the mullet, *Mugil cephalus,* remained all winter.

The catch of brown shrimp, *Penaeus aztecus,* was also similar to that Gunter (1950a) found in Copano Bay. In Mesquite Bay there were two peaks of abundance, one in June and a much smaller one in November. Gunter also found two peaks in abundance, but the numbers he took in Aransas Bay during both peaks were nearly equal, while the numbers in Copano were much greater in June as in Mesquite Bay. The fall peak in shrimp stocks was in October, 1941, but temperatures for Copano Bay in that month were more similar to November temperatures in Mesquite Bay.

In the fish trap study conducted while Cedar Bayou was open more stenohaline marine fishes were taken. Gunter (1954a) and Reid (1956a) both found stenohaline fishes near Aransas Pass and Rollover Pass.

Ninety-two species of fishes were taken while Cedar Bayou was open and 73 while Cedar Bayou was closed. The latter includes several nonmigratory species which were probably present but not taken while Cedar Bayou was open. It is interesting to note that tarpon (*Megalops atlanticus*) were not taken or seen while Cedar Bayou was closed. Since the species is euryhaline (Gunter, 1956), low salinities encountered while Cedar Bayou was closed do not explain their absence. Extensive netting in the summer of 1957 when tarpon are in the bays (Springer and Pirson, 1958) did not yield a specimen.

Invasion During the Washover from Hurricane Audrey

While Cedar Bayou was inundated by the tides from Hurricane Audrey from June 27 to July 1, 1957, certain fishes and invertebrates apparently entered and salinities rose

to 20.4–20.8 ppt. These either had not been in the area or were uncommon during the month of June when salinities were below 5 ppt in the bay and below 10 ppt in the bayou. The species found in Cedar Bayou on July 1, at stations 12, 13, and 14 are listed as follows with the total number collected shown in parenthesis:

Callinectes danae (240); *Libinia dubia* (2); *Caranx hippos* (1); *Chaetodipterus faber* (1); *Monacanthus hispidus* (2); *Pagurus floridanus* (3); *Polynices duplicata* (1); *Chloroscombrus chrysurus* (2); *Ancylopsetta quadrocellata* (2); *Alutera schoepfi* (2); and *Chilomycterus schoepfi* (1).

Of these species that entered only *Chaetodipterus faber, Ancylopsetta quadrocellata,* and *Pagurus floridanus* were subsequently taken in either the bay or bayou. Other species taken in the same collection may have entered with the washover, but this entry cannot be shown as they were present during June.

Summary

1. Two studies were conducted on Cedar Bayou, a former natural inlet on the Texas Coast, one in 1950–1951 with the inlet open, and one in 1957–1958 with the inlet closed.

2. The past history of the mouth of Cedar Bayou indicates that river discharge of the Guadalupe River System is the important factor in the maintenance of the inlet.

2. While Cedar Bayou is shoaled, salinity is controlled by river discharge and by winds, particularly northers.

4. Eighty-five per cent of fishes taken in two-way traps in Cedar Bayou were moving gulfward in 1950–1951. The most abundant fish taken was *Micropogon undulatus.*

5. *Cynoscion nebulosus* moved to the gulf through Cedar Bayou with sudden drops in water temperature. The average size of trout increased from May through September.

6. Large individuals of *Sciaenops ocellatus* apparently did not enter bays but smaller sub-adults did.

7. *Paralichthys spp.* moved through Cedar Bayou to the gulf in large numbers in the fall and the young moved bayward in the spring.

8. Large numbers of penaeid shrimp and blue crabs passed through Cedar Bayou.

9. The fauna of Cedar Bayou differs from that of Mesquite Bay. The two areas differ also in bottom type, depth, and salinity.

10. It is concluded that immigration is delayed nearly one month when Cedar Bayou is closed compared to the schedule when the bayou is open to the gulf. The annual cycle in fish populations in Mesquite Bay while Cedar Bayou was closed were similar to that in secondary bays.

11. It is concluded that when open Cedar Bayou (1) may be of some value for escapement of fishes during cold weather; (2) may be important to the immigration and subsequent development of young penaeid shrimp; (3) may diminish oyster mortality by flushing out fresh water at flood time, (4) may introduce more stenohaline fish, oyster predators and competitors, especially in Cedar Bayou; and (5) may increase the opportunities for fishing by man along the pass.

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Survival of F_1 Hybrids Between Cyprinodont Fishes, With a Discussion of the Correlation Between Hybridization and Phylogenetic Relationship

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Abstract

Hybrids were produced by artificially mixing the gametes of five cyprinodont fishes. Hybrid survival varied dependent upon which species was the maternal parent. *Fundulus similis* by *F. grandis* hybrids did not survive the hatching period if *F. similis* eggs were used, but survival of the reciprocal was very high. Greater hybrid survival was obtained when the parents were more closely related. Although survival was low, one *Fundulus* by *Cyprinodon* hybrid hatched and ingested food.

These results correlate with those reported by other authors, that the level of development of hybrids correlates with the relationship of the parental species. A few apparent discrepancies involve hybrids whose parents are probably more closely related than shown in current taxonomic references.

Introduction

Hybrid formation is common in fishes. Not only are many laboratory hybrid combinations possible (Moenkhaus, 1910) but also many natural hybrids are known (Hubbs, 1955). Both authors have noted that the capacity to hybridize is correlated with the degree of parental relationship. Moreover, Hubbs and Strawn (1957a) have pointed out that the ability to produce laboratory hybrids correlates closely with the known natural hybrids in the subfamily Etheostomatinae.

Many laboratory hybrids have been produced among species of the viviparous poeciliids (Hubbs, 1955; Gordon, 1957, however, much of the work is unpublished) and oviparous cyprinodontids (Newman, 1914; for North American forms and Öztan, 1954, for Turkish forms). Newman showed that interspecific hybridization is possible and Öztan reported on hybrids between members of related genera. More or less comparable results have been obtained from known natural hybrids (Hubbs, Walker, and Johnson, 1943). They reported interspecific hybrids as well as hybrids between closely related genera. Our results are similar to those of Öztan and especially Newman, who worked at Woods Hole, Massachusetts where the cyprinodont fauna is less diverse than that near Port Aransas, Texas. Our data, thereby, differ somewhat due to the additional species used so that hybrids between related genera were produced and a hybrid between members of two commonly recognized subfamilies hatched and fed.

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Methods

Parental fish were obtained in the vicinity of Port Aransas, Tex. They were maintained in running water aquaria and fed on a variety of crustaceans and fish. Gametes were stripped from the parents and the zygotes cultured following techniques described by Strawn and Hubbs (1956), except that glass preparation dishes were used instead of enamel trays. Temperatures ranged between 26° and 31°C. Salinities were around 30 ppt.

Eggs and young were examined daily or more often. When necessary eggs were microscopically checked. Following Hubbs and Strawn (1957a), development was first recorded when pigment occurred in the eyes. This procedure reduces misinterpretation through the possible effect of gynogenetic development stimulated by sperm, or purely maternal development resulting from elimination or inactivity of paternal chromatin. All hybrids reared to any appreciable size were intermediate between the parental phenotypes and, therefore, showed some effect of paternal chromatin. Moreover, hybrid combinations often had ontogenetic rates different from that of the maternal controls. Therefore, we feel that we are dealing with hybrids.

Because of adverse laboratory conditions (primarily high temperature) males often did not produce visible milt. Therefore, non-fertilization may be due to experimental conditions. This is especially pertinent since many controls had low fertilization percentages. Thus, only the number of developing eggs is considered significant.

Experimental Crosses and Hybrid Survival

Fundulus grandis Baird and Girard by F. similis (Baird and Girard) hybrids.—Very different results were obtained from the two reciprocals (Table 1). Those based on *F. grandis* eggs were successfully reared, whereas those based on *F. similis* eggs did not hatch. These results are identical to those obtained by Newman (1908; 1914) and Moenkhaus (1910) for hybrids between *F. heteroclitus* (Linnaeus) and *F. majalis* (Walbaum) which are sibling species to *F. grandis* and *F. similis* respectively (Miller, 1955). Adequate data are not available to determine whether *F. grandis* ♀ × *F. similis* ♂ hybrids show heterosis; however, the fastest growing *Fundulus* in our laboratory is a hybrid.

Fundulus grandis by Lucania parva (Baird and Girard) hybrids.—Different results were obtained for the two reciprocals of this cross (Table 1). Although this may be due to sample size, the differences are probably biologic as each combination was based on two or more fertilizations and the results were consistent. Hybrid survival was lower than that of either control and the *F. grandis* ♀ × *L. parva* ♂ cross did better than the reciprocal of which no fish survived the larval stages.

TABLE 1

Survival of Cyprinodont hybrids and ocntrols at about 28° C and 30 ppt salinity

Paternal parent	Number of eggs stripped	Number of eyed eggs	Number of eggs hatched	Number of young through larval stages	Days to hatch	Notes
			Eggs from *Fundulus grandis*			
Fundulus grandis	805	259	257	247	9–13	
Fundulus similis	49	5	5	3	11–18	
Lucania parva	474	62	37	20	7–14	
Adinia xenica	23	6	0	0	....	Died 13th to 26th days
Cyprinodon variegatus	370	13	5	0	8, 14, 15, 15, 18	Last fed and lived one week
			Eggs from *Fundulus similis*			
Fundulus similis	10	3	3	3	14	
Fundulus grandis	169	26	1(dead)	0	14	Most eggs died 17th to 21st days
			Eggs from *Lucania parva*			
Lucania parva	18	7	4	4	6–9	One death accidental
Fundulus grandis	6	3	2	0	8–13	
			Eggs from *Adinia xenica*			
Fundulus grandis	18	13	8	6	15–16	
Cyprinodon variegatus	4	2	0	0		Died 9th day
			Eggs from *Cyprinodon variegatus*			
Cyprinodon variegatus	243	43	39	16	4–5	Many died of starvation

Fundulus grandis by Adinia xenica (Jordan and Gilbert) hybrids.—Only one experiment is available for each reciprocal and markedly different results were obtained (Table 1). *F. grandis* ♀ × *A. xenica* ♂ hybrids did not hatch and the reciprocal had a much lower survival than that of *F. grandis*, the only control.

Fundulus grandis by Cyprinodon variegatus Lacépède hybrids.—Fertilization occurred only in *F. grandis* ♀ by *C. variegatus* ♂ crosses (Table 1), although the reciprocal was tried three times without fertilization. Two of the embryos were much larger than the other 11 and had a developmental rate similar to that of *F. grandis*. The large embryos did not hatch and were deformed at death. The small embryos were also deformed. The one that fed had a distended and apparently normal gut. It had a well-developed caudal and both pectorals but no sign of other fins. In addition, the fish had an upward postoccipital hump, the body axis bent ventrally at a right angle at the level of the anus and on the caudal peduncle the axis bent sharply to the right. These deformities are present not only in the preserved fish, but also were noted when the fish was alive. Nevertheless, the fish is intermediate is some structures so that its development must have been influenced by both maternal and paternal genes. The head shape is intermediate between that of *F. grandis* and the more robust *C. variegatus*. The mid-ventral peritoneum is dark but the melanophores are less widely distributed than in *C. variegatus*. *F. grandis* young have a light peritoneum. The opercular melanophores in the hybrids are more scattered than in *F. grandis* and less scattered than *C. variegatus*. The mid-dorasl dark band is wider than that of *F. grandis*, but narrower than that of *C. variegatus*.

All of these hybrids passed through more ontogenetic stages than did Newman's (1914) *Fundulus* × *Cyprinodon* hybrids, most of which died at or before gastrulation. The greatest development he reported was to the end of gastrulation. Our success was either fortuitous, due to the use of *F. grandis* eggs which were not available to Newman, or due to true fertilization. Newman's results may have been based on gynogenetic development.

Adinia xenica by Cyprinodon variegatus hybrids.—The two fertilized eggs of this combination failed to hatch (Table 1). We suspect that it would be possible for this hybrid to do as well as that between *F. grandis* and *C. variegatus.*

Hubbs (1955) emphasized the great difference in natural hybrid frequency of fresh- and salt-water fishes. He indicated that the salt-water environment is more stable than the fresh-water habitat and used this fact as a partial explanation for the difference. Hybrid inviability and associated phenomena may also partially explain the relative infrequency of natural hybrids among marine fishes. Almost any hybrid combination is possible between members of the fresh-water subfamily Etheostomatinae (Hubbs and Strawn, 1957a) and hybrid survival is equal to or greater than that of the controls. Our results with hybrids between members of the subfamily Fundulinae differ markedly in that most hybrids have a survival less than that of the controls (Table 1). Newman (1914) also reported reduced viability and vigor of some *Fundulus* hybrids in addition to those reciprocals that never hatched. Like Newman, we find some hybrid combinations that have survival values equal to or greater than those of the controls. Perhaps such natural hybrids are unable to find a suitable ecologic niche for growth to adult size if and when other isolation mechanisms break down.

Our results differ from previous work done on darter hybrids at The University of Texas in that radical differences occur in the survival of cyprinodont reciprocals, while darter reciprocals are essentially similar.

Egg Size and Differential Survival of Reciprocal Hybrids

The differences in hatching of hybrids between reciprocal crosses of the small-egged species, *F. heteroclitus*, and the larger-egged species, *F. majalis*, were correlated with egg size by Newman (1908). He felt that the *F. majalis* ♀ × *F. heteroclitus* ♂ hybrids failed to hatch "because of their inability to consume the large mass of superfluous yolk." He repeated but somewhat modified his conclusion in 1914 by stating that "the difficulty is almost certainly one involving retarded or partial yolk assimilation." This conclusion was based on previous results and data from reciprocals between another small-egged species, *F. diaphanus* (LeSueur), and the larger-egged species, *F. majalis.* Some of our results show the same pattern, while others show the converse. For example, hatching occurs when the egg is from the small-egged species, *F. grandis*, and hatching does not occur when the egg is from the larger-egged species, *F. similis.* Moreover, *A. xenica* has an egg that is smaller than that of *F. grandis* and hatching in this hybrid combination occurs when the small *A. xenica* egg is used but not in the reciprocal which is based on the somewhat larger *F. grandis* egg. Although these data tend to support a correlation of success with egg size, other crosses give contradictory results. *F. grandis* eggs hatch when fertilized with sperm of *L. parva* and *C. variegatus*, both of which have much smaller eggs. Moreover, the reciprocal of both crosses did not succeed nearly as well. It is also possible that the cytoplasm of *F. similis* and *F. majalis* eggs is incompatible with foreign paternal chromatin. As these two species are closely related, this attribute may stem from their common ancestor. However, one of our apparent failures is with eggs of *F. grandis*, a species rather distantly related to *F. similis* and *F. majalis.* Probably the reason for differential survival of reciprocals involves incompatibility of the maternal cytoplasm with enzymes produced by the paternal chromatin or vice versa.

This probably becomes most critical late in ontogeny when the paternal chromatin is more influential on development.

Time of Hatching

Moenkhaus (1910) stated that foreign sperm delayed the hatching of eggs. Newman (1914) believed that the time of hybrid hatching typically was intermediate between that of the two parental forms. Hubbs and Strawn (1957a) reported that darter hybrids developed at rates similar to that of their maternal controls; however, the differences between the parental rates were minor. Our results indicate that the hybrids hatch over a much longer interval than either control (Table 1). The first hybrids to hatch typically do so at a time intermediate between that of the parental controls (following Newman's conclusion) and the last hybrids to hatch take much longer than either control (following the conclusion of Moenkhaus). Apparently if the parental forms have different rates of development the hybrids may hatch from an intermediate time to one much later than either control.

Correlation of Degree of Relationship with Capacity to Hybridize

Moenkhaus (1910), Hubbs (1955), Alm (1955), Buss and Wright (1956 and 1958), Suzuki (1957a, b, and c), Kobayasi (1957), and Hubbs and Strawn (1957a) have noted that the capacity to hybridize is correlated with the degree of parental relationship. Workers on other animals have likewise noted such a correlation (Patterson and Stone, 1952; Gray, 1953; and Moore, 1955). Newman (1914), however, believed that capacity to hybridize was not correlated with phylogenetic relationship. He based this conclusion on two sets of data. The first was the difference in success between the two reciprocals of certain *Fundulus* hybrids. Recent work on *Drosophila* has shown, however, that occasional inviability of hybrids may occur between closely related species or even between individuals of the same species (Patterson and Stone, 1952). Obviously such unusual examples do not negate the general hypothesis.

Maternal Inheritance of Interfamilial Hybrids.—Newman's other reason for proposing that capacity to hybridize is not correlated with phylogeny was the development of "hybrids" (our quotes) between distantly related fishes, including species that belong to different orders. We feel that many of these are not necessarily true hybrids, but are of maternal origin. Most interordinal "hybrids" die during gastrulation. Loeb (1912) produced late embryos when he treated *F. heteroclitus* eggs with weak NaCN solutions. These embryos resembled some of those supposed to be hybrids. Moreover, Buss and Wright (1956) reported a brook trout embryo with a haploid chromosome number that must have been of maternal origin. Similarly, eggs are laid by, or can be stripped from, female darters in the absence of males. Occasionally these eggs will begin cleavage. All such eggs die during gastrulation (Linder, 1958, and our own observations) and are therefore considered to be gynogenetic. Both Moenkhaus and Newman had controls, stripped from the female, that did not develop; however, these eggs were not exposed to jarring as were experimental eggs when "fertilized" by foreign sperm. The eggs we used were jarred and those used by Linder were laid naturally. Thereby, "hybrids" that die at

gastrulation may be gynogenetic unless paternal chromatin is found cytologically. We suspect Newman's failure with *Fundulus* by *Cyprinodon* hybrids lies here.

Even if the sperm nucleus enters the egg its effect may be negligible on the resulting embryo. Hertwig (1936) listed many examples of entire or partial elimination of paternal chromatin during early cleavage as well as the absence of paternal characters in the embryos. As she had pointed out these embryos are false hybrids (Falsche Bastarde). Morris (1914) and Pinney (1918, 1922, and 1928) have shown that many of the interordinal teleost crosses show elimination of paternal chromatin during early cleavage. Many of the crosses that do not lose the paternal chromatin die in early embryonic stages. Those interfamilial hybrids that do develop to advanced embryos are either primarily maternal or between closely related parental forms. Obviously, embryos with primarily maternal chromatin are false hybrids and the degree of their development is not significant to a correlation between hybridization and phylogeny.

Guthrie (1925) studied the cytoplasm of several eggs that had been fertilized with sperm of the same and different species. Unfortunately, all but one of her hybrid combinations were those shown by others to have normal mitosis. She did find that the effect of paternal chromatin was most noticeable when closely related species were crossed; however, her study was limited to only four species, and only half of the potential hybrid combinations among them were tested. Undoubtedly, paternal enzymes are most effective on the cytoplasm when the species (and chemical substrates) are most closely related. Thus, the effect of paternal chromatin is not great during early embryology of crosses between distantly related species, again a correlation of hybridization with relationship.

Rubinoff and Shaw (1958) showed that the two reciprocals of an intrageneric atherinid hybrid combination differed morphologically. Each approached the maternal parent in the character analyzed, thereby indicating a possible partial inactivity of the paternal chromatin as well as influence of egg cytoplasm on the offspring.

All but two of the multitude of interfamilial crosses made by Moenkhaus (1910) and Newman (1915) did not complete their embryonic development or can be questioned as being either gynogenetic or as being complete or partial false hybrids. Only two of those that developed to hatching have been shown to have paternal chromatin or paternal phenotypic characters. Newman's (1915; 1918) analysis of the phenotypes of different embryos of a single cross supports this hypothesis. Individuals of several "interfamilial" combinations that hatched showed maternal inheritance, while those that died earlier in ontogeny had paternal characters. Thereby, the successful individuals were primarily maternal and the unsuccessful ones were hybrids.

INTERFAMILIAL HYBRIDS.—Pinney (1928) ascribed normal mitosis to two interfamilial crosses that hatched. One was between *Tautogolabrus adspersus* (Walbaum) = *Ctenolabrus adspersus* ♀ and *Stenotomus versicolor* (Mitchill) = *S. chrysops* (Linnaeus) ♂. The two species are typically placed in the families Labridae and Sparidae, respectively. Pinney followed Jordan and Evermann (1898) and placed the two families in different suborders. However, both Regan (1913a) and Berg (1947) placed them in the same suborder but in different divisions or superfamilies. Thus, the parental forms are now considered more closely related than given by Pinney.

The other hatched interfamilial hybrids listed by Pinney are both reciprocals between *Fundulus heteroclitus* and *Menidia notata* (Linnaeus). These results are not fortuitous as Moenkhaus (1910) and Newman (1915) also had success with these hybrids and

Clark and Moulton (1949) had both reciprocals of the related *F. heteroclitus* by *Menidia beryllina* (Cope) hybrid reach late embryonic stages. *Fundulus* and *Menidia* belong to the families Cyprinodontidae and Atherinidae and these families are assigned to different orders, Cyprinodontiformes and Mugiliformes, respectively, by Berg (1947). As cyprinodonts are soft-rayed fishes and atherines have spines in their fins, early classifiers considered the two groups distantly related. Other workers, notably Regan (1911), Hubbs (1920; 1924; 1955; 1950), Gregory (1953), Boldyreff (1935, and Lagler (1947) have suggested that cyprinodonts are closely related to the spiny-rayed fishes and perhaps are descendants of primitive spiny-rayed fishes. Cope (1870) and Myers (1928) mentioned the similarity between the atherines and cyprinodonts and questioned the difference between them implied in systems of classification then (as now) in vogue. Moreover, the phallostethid fishes have been placed with the cyprinodonts by Regan (1913b; 1916), Weber and de Beaufort (1922), Jordan (1923), Hubbs (1924), and Herre (1926), while Herre (1939; 1942), Myers (1928, 1935; 1937), Bailey (1936), Aurich (1937), Te Winkel (1939), and Hubbs (1944) allied them with the atherines, and Berg (1947) placed the phallostethids in a separate order close to the cyprinodonts. Similarly, *Basilichthys semotilus* (Cope) has been placed in the Mugilidae (Cope, 1874), Cyprinodontidae (Cope, 1875), and Atherinidae (Jordan, 1923). These changes in the taxonomic allocation of the phallostethids and *B. semotilus* suggests a closer relationship of those fishes than that implied by current classifications. This is supported by the data derived from hybridization experiments. Thus, the *Fundulus* by *Menidia* hybrids actually may not be interordinal.

Interfamilial hybrids have also been studied by more recent workers. Suzuki (1953, 1955, 1956, 1957a, and 1957b) had much success hatching hybrids between various species of the closely related families, Cobitidae and Cyprinidae. He made numerous unsuccessful attempts to make interordinal or interclass crosses. Suzuki's interfamilial hybrids died as larvae, apparently without feeding. Most of the numerous intrafamilial hybrids, studied by Suzuki, fed and were reared to apparent adult size. Hubbs and Strawn (1957a) also were able to hatch hybrids between various species of two closely related families, Centrarchidae and Percidae, all of which died shortly after hatching. However, many intrafamilial hybrids were reared to apparent adult size. Thereby, it is possible that interfamilial hybrids may hatch but do not feed whereas intrafamilial hybrids hatch and feed.

Rubaschev (1935) reported on hybrids between members of the genera *Salmo* and *Coregonus*. None of them hatched. These failures support Jordan's (1923) separation of the two groups on the familial level.

Intertribal Hybrids.—There is little doubt that the *Fundulus* by *Cyprinodon* hybrid is intrafamilial, however, the taxonomic separation of the parental forms within the family is less certain. Hubbs (1924), Myers (1931), and Berg (1947) consider the parental types to belong to different subfamilies, however, Miller (1956), on the basis of adult morphology and Öztan's (1954) hybridization experiments, believes that the subfamilies should be united. Our success with this hybrid supports Miller's conclusion and also indicates that *Fundulus*, *Adinia*, and *Lucania* are more closely related to each other than any is related to *Cyprinodon*. Perhaps the taxonomic separation should be on the tribal level.

More work on differential hybrid survival is necessary before conclusions on supergeneric classification can have more than tentative value. Moreover, taxonomic ranking

should be based on an evaluation of all available evidence, not primarily on any single one such as that of hybridization. However, in each of the examples discussed above, taxonomists are debating the relationships based on morphologic grounds, whereas, the hybridization data are objective.

INTERGENERIC HYBRIDS.—Hybrid fertility also appears to be related to the degree of phylogenetic relationship. As such experiments require rearing of hybrids and controls, all too few studies are now available. However, the majority of the reports do show a correlation between taxonomic separation and hybrid fertility and most of the fertile hybrids are between parental forms commonly placed in the same genus (Alm, 1955; Hubbs, 1955; Hubbs and Strawn, 1956; Lagler and Steinmetz, 1957; Gordon, 1957; Hubbs, 1958; Buss and Wright, 1958). Only Öztan (1954) and Minamori (1957) have reported even rare fertility of intergeneric hybrids. Many workers (Öztan, 1954; Alm, 1955; Hubbs and Strawn, 1957b; Buss and Wright, 1958) have found infertile intergeneric hybrids. Such negative evidence needs to be confirmed since the results obtained by Hubbs and Hubbs (1932) differed from those of Lagler and Steinmetz (1957), probably due to the different parental populations used. Hybrid fertility might be considered as an indication of congeneric relationship and consistent infertility between many species as an indication of generic separation.

The levels of taxonomic ranking, given to these abilities to produce fish hybrids, is greater than that for other groups of organisms. Working with higher plants Clausen, Keck, and Hiesey (1945) considered gene exchange an attribute of members of a cenospecies and that such exchange was rare or impossible between members of different cenospecies. Clausen (1951) regarded the taxonomic ranking of cenospecies to be subgeneric. He also separated genera by their inability to readily produce hybrids. Working with *Drosophila*, Patterson and Stone (1952) were even more conservative in that they rank parents of hybrids in the same species group. Probably hybridization abilities vary between major groups of organisms and perhaps even between relatively closely related organisms.

Summary

1. Fertilization was achieved for five cyprinodont hybrid combinations, three of which include both reciprocals. Successful hatching occurred in the following combinations (maternal parent listed first): *Fundulus grandis* × *F. similis*; *F. grandis* × *Lucania parva*; *F. grandis* × *Cyprinodon variegatus*; *L. parva* × *F. grandis*; and *Adinia xenica* × *F. grandis*. Hatching did not occur in the following combinations: *F. grandis* × *A. xenica*; *F. similis* × *F. grandis*; and *A. xenica* × *C. variegatus*. Successful completion of the larval stages was attained by the following hybrids: *F. grandis* × *F. similis*; *F. grandis* × *L. parva*; and *A. xenica* × *F. grandis*. Except for the *F. grandis* × *F. similis* hybrids, controls had much greater survival than the hybrids.

2. Every hybrid combination that did not hatch was based on eggs of a larger-egged species and sperm of a smaller-egged species. However, many that did hatch had parental forms with the same egg-size relationships. Hybrids varied greatly in hatching time, the first doing so after an interval intermediate between that of the parental forms and the last hatching long after the last control.

3. Many apparent hybrids between distantly related fishes are discounted because there is no evidence of any influence of paternal chromatin.

4. Hybridization often correlates with suspected degree of phylogenetic relationship based on morphologic studies. Apparent discrepancies are often due to chance or occur in groups in which morphologists disagree about the relationships. Although much more work is necessary to verify the tentative conclusions, four hypothetical levels are suggested:

Hatching — intraordinal:interfamilial
Feeding — intrafamilial:intertribal
Rearing — intratribal:intergeneric
Fertility — intrageneric:interspecific

Obviously hybrids between more closely related groups generally can exceed the level limiting hybrids between more distantly related fishes.

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Some Observations on the Respiration of the American Oyster *Crassostrea virginica* (Gmelin)[1]

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Abstract

The Krogh syringe and some analytical improvements by Pomeroy and Kirshman in the Winkler method for oxygen analysis were combined with the direct method of measuring the pumping rates of the oyster to obtain data on oxygen uptake at various pumping rates. When pumping at a rate of 25 liters per hour an oyster may consume as much as 50 mg of oxygen per hour. The rate of oxygen removal from the water in mg per liter per ml of shell cavity plotted against pumping rates is parabolic. When the hourly work output for various pumping rates are compared with a theoretical curve, it is found that the oyster can pump water at approximately 10 liters per hour with a maximum efficiency of 10 per cent. An oyster with a shell cavity of 40 ml can pump over 40 liters per hour but at this rate the efficiency falls to less than two per cent. Some unknown carbohydrate-like substances are removed from the water in quantities commensurate with the oxygen uptake. The role of algae in the energy budget of the oyster as reflected by oxygen uptake is discussed, and certain points relative to the production of extracellular carbohydrates by algae are considered.

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Introduction

The quantity of oxygen consumed by an animal is related to such metabolic processes as growth, repair of tissue, excretion, digestion, and osmoregulation. Besides these basic processes, any act, which results in the performance of mechanical work, increases con-

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sumption. In the oyster, for instance, there are shell movements and the pumping of water through the branchial chambers; activities necessary for respiratory and feeding purposes. Associated with the latter there is often a great production of mucus which entrains silt and other dejecta, the whole being voided as pseudo-feces. Both the production of this mucus and the work done by the ciliated epithelium in transporting it entails an additional demand for oxygen.

Water pumping and the associated activities of the oyster are analogous to food hunting on the part of non-sedentary animals. But since, as a sedentary animal, the oyster cannot search for favorable feeding areas it should (1) expend energy only when the water being pumped contains sufficient available nourishment to allow a net gain of energy over that required by the work being done and (2) be able to accumulate a reserve of potential energy which can be drawn on in times of famine and to augment the development of gonadal tissue as the spawning season approaches.

These two phases of the oyster's struggle for existence impel its complete integration with its immediate environment. The first has been quantitatively assessed only in recent years (Collier *et al.*, 1953) and is, in effect, a method of conserving energy. The second, the storage of energy in the form of glycogen, has been long established and is largely responsible for the commercial value of oysters.

To understand the natural factors which cause fluctuations in the abundance and condition of oysters it would be useful to know how much work is done by the oyster in pumping water and how the resulting respiratory and nutritional requirements are related to environmental factors. The most expedient means of measuring the work performed by an organism is to estimate the amount of oxygen consumed per unit of time per unit of respiring tissue. This has been done for a number of invertebrate animals and several studies have been made on the oxygen uptake of oysters.

Mitchell (1914) and Galtsoff and Whipple (1931) published the first reports on the oxygen uptake of American oysters. The principle of the experimental technique, in both cases, was the measurement of the differences between the initial oxygen content of a mass of standing water containing the oysters and samples drawn at succeeding intervals. Galtsoff and Whipple concluded from these experiments that the oxygen varied from 6.45 to 15.04 ml (760 mm Hg, 0°C) per hour per 10 grams of dry weight. No attempt was made to measure the uptake as related to pumping rate but kymograph traces were made of shell movements. The movements illustrated in his paper were not typical of normal pumping oysters. Mitchell's results were 0.35 to 1.29 mg per hour per gram of dry weight; reduced to the same terms, Galtsoff and Whipple's results were 0.92 to 2.1 mg per hour per gram of dry weight. Jørgensen (1952) made correlative studies of respiration and pumping rate. To estimate the pumping rate he used the indirect method of Fox (1937) while oxygen levels were estimated by the Winkler method. Jørgensen concluded that his oysters pumped 10 to 20 liters of water for each milliliter of oxygen consumed. This frame of reference does not permit reduction of the data in terms of variable pumping rates and amounts of respiring tissue.

Observations on oxygen uptake made simultaneously with the measurement of pumping rates by the direct method are reported for oysters obtained at Pensacola, Florida.

I wish to acknowledge the assistance of my co-workers, Dr. Sammy Ray and Mr. A. W. Magnitzky, whose industry and expert attention to detail made this work possible.

Methods, Materials, and Terminology

The Determination of Dissolved Oxygen

For many years the Winkler method has been the standard method of estimating the quantity of oxygen dissolved in water. Krogh (1935) introduced a modification utilizing syringe pipettes and correspondingly small samples. Yoder and Dresher (1934) studied the effects of oxygen contained in reagents and tested the various types of starches as end-point indicators. After studies of the solubilities of sodium iodide in sodium hydroxide solutions (Pomeroy and Kirshman, 1944), and potassium iodide in potassium hydroxide solutions (Kirshman and Pomeroy, 1943), and potassium iodide in sodium hydroxide (Kirshman and Pomeroy, 1944), Pomeroy and Kirshman (1945) suggested a modified Winkler method which we combined with the Krogh syringe pipette method for use in these studies. The modification was chiefly in the high iodide concentration for which Pomeroy and Kirshman claimed the following advantages: less interference from other reducing agents, reduced loss of iodine vapor, and a sharper end-point. The routine procedure used in these experiments follows.

A set of 10 ml syringes were prepared and calibrated according to the method of Krogh (1935).

The solutions were as follows:

I. 90 grams of NaI and 40 grams of NaOH in 55 ml of water.

II. 40 grams $MnCl_2$, and 10 ml 6N HCl made up to 100 ml with water.

III. 6N HCl.

IV. 0.003572 N sodium thiosulfate. Standardized with standard solution of $K10_3$ or recrystallized potassium dichromate.

V. Starch in saturated NaCl.

Reagents I and II were kept in rubber capped vaccine bottles. The routine determinations were performed as follows:

1. Syringe needle (18 gauge) inserted through rubber cap into inverted vial containing Reagent I. Reagent drawn in and expelled by pushing plunger to bottom of syringe. All air bubbles expelled. This left about 0.1 ml of solution in dead space of syringes.

2. Water sample and Reagent I left in dead space; drawn in by pulling plunger back to first stop.

3. After water sample drawn, syringe held in inverted position and care taken not to collect air bubbles. Needle inserted through rubber cap of vial containing Reagent II. Plunger withdrawn to second stop. The $MnCl_2$ reacts with the NaOH originally in the dead space and subsequently mixed with the sample to produce a precipitate of manganous hydroxide which absorbs all of the oxygen dissolved in the water in about five minutes.

4. After the five minute waiting period, discharge the contents of the syringe beneath the surface of 1 ml of 6N HCl. The syringe was rinsed with the acid solution and then with two rinses of water.

5. Titrate with microburette. 1 ml of Reagent IV equals 0.02000 ml of oxygen (0°, 760 mm).

To determine the amount of oxygen removed from the water by an oyster, a sample was taken from the inhalant side and at the same time from the exhalant side. The difference in the oxygen concentration of the two samples indicated the removal rate. The syringe needles were brought as close to the apertures as possible without causing the oyster to close.

This method of collecting the oxygen samples was similar to that originally described by van Dam (1954), and was subject to certain errors pointed out by him. He showed that different oxygen values could be obtained by placing the syringe tip at different points in the exhalant stream. Such errors probably entered these data and were possibly responsible in part for some of the aberrant points obtained.

Methods of Measuring and Recording Pumping Rate

The experimental apparatus used for recording the pumping rates of oysters has been described elsewhere (Collier and Ray, 1948 and Collier *et al.*, 1953). The method was a combination of the rubber dam and the constant level tank. This is a direct method of measurement to which certain objections are commonly raised. The criticisms center around the attachment of the rubber dam and the possible interference with shell movements which may be caused. Any experimental method is subject to such criticisms, but I can offer evidence that these oysters were not overburdened by the artificial environment under which they were kept. During these experiments the oysters were maintained in the experimental apparatus for months at a time and in some cases substantial growth occurred. For instance, an oyster placed in the apparatus on January 23 increased in length 15.5 mm and in total volume 17.5 ml by June 23. Under the experimental conditions imposed, this particular oyster exhibited a maximum pumping rate of approximately 35 liters an hour. Other animals, although not retained as long, showed signifigrowth and exhibited pumping rates over 40 liters per hour.

The samples for oxygen determinations were all drawn while the oyster was pumping water. In addition to the automatically recorded pumping rates, the rates were directly determined for the precise moment that the oxygen sample was drawn by collecting the exhalant water in a graduated cylinder.

The Oysters

The oysters used in these experiments came from various localities around Pensacola, Florida. The individuals were initially selected according to the adaptability of their shape to the attachment of the rubber dam and their freedom from boring organisms. Their condition could not be determined until a sufficient record of their valve and pumping activities was made. Even then their glycogen content, freedom from disease, and internal parasites could not be ascertained. As the work progressed, the investigator recognized a normal pattern of activity which was characteristic of those animals showing significant growth and maximum pumping.

Terminology

In work of this nature, dry weight of the respiring tissue is ordinarily used as the common denominator for the comparison of animals of different sizes. In this case the observations for a given individual were made over a long period of time and determi-

nation of the dry weight of the tissues prior to the completion of the experiment was impossible. Because of the variability in the glycogen content, the state of the gonads during the spawning season, and a variety of other physiological factors, the weight of the meat at the end of the experiment would have had little meaning relative to the pumping function throughout the long experimental period. The volume of the shell cavity was used as the best available measurement providing some degree of constancy. In examining the data and making interpretations, the source of error in using cavity as a measure of the animal's average volume is to be borne in mind.

The volume of the shell cavity for calculations was determined by the difference between the total volume of the intact oyster and that of the valves after the meat was removed; both volumes were obtained by displacement measurement. The primary data are reduced to milligrams of oxygen per liter of water (at a specified pumping rate) per milliliter of shell cavity.

The transport of water through the branchial systems of sedentary filter feeders has been designated by the terms "filtration rate," "feeding rate," and as I have done here, "pumping rate." Filtration infers that the animal may be filtering water but not necessarily feeding, while "feeding rate" implies actual feeding. By definition, pumping rate implies neither. It has not been shown that all water which is transported through the body of an oyster has been filtered; it is possible that part is passed through for respiratory purposes. I have used "pumping rate" throughout this paper to connote the total water passed through the body of the animal without designating whether it is filtered for food, just filtered, or utilized as a respiratory medium.

In the analysis of the data which follows it will be necessary to refer to the types of shell movement. These are Phases I, II, and III described by Collier *et al.* (1953). Phase I is the brief period during which the valves move from the position of complete closure to the degree of gape characteristic of the testing period or Phase II. During Phase I there is often a dripping of water from the exhalant side of the animal which is difficult to sample. This is probably water which was entrapped by the valves when they closed. This fluid, when successfully collected, was always nearly depleted of oxygen. In Phase II the valves are only partly opened and the pumping rate fluctuates between about 4 and 12 liters per hour. The above authors regarded this as a "testing period" because they observed that if certain unknown substances responding to the N-ethyl-carbazole test for carbohydrates were not above threshold levels the animal would close without going into Phase III, or the phase of active pumping. Phase III was characterized as one in which the maximum gape and maximum pumping rates occurred. For example, an oyster with a shell cavity of approximately 40 ml pumped over 40 liters an hour during this phase.

Sea Water Conditions

Our experimental arrangements did not include provisions for controlling temperature or salinity. The sea water circulating system drew water directly from Santa Rosa Sound, Florida. Temperature and salinity were determined regularly, but the influence of pumping rates of the oysters on oxygen uptake proved to be so great that the effects of other factors were obscured. There were undoubtedly some variations due to salinity, temperature, and viscosity but our data are not sufficiently abundant to demonstrate their effect. The discussion of the experimental results will, therefore, be confined to oxygen uptake and pumping rate only.

Experimental Results

Oxygen Uptake From Pumping Rates

The results from the four oysters, on which we obtained the greatest amount of information and the most consistent data, are presented in A and B of Figure 1. For this group of animals the most noticeable attribute common to all four cases (curves A and B) is the tendency for the points to group roughly along the locus of a parabola. Since the lowest pumping rates generally follow periods of closure, oxygen tends to be removed from the water more rapidly at the lower pumping rates with a decreasing rate of removal as the flow rate of the water increases. The total oxygen removed from the water

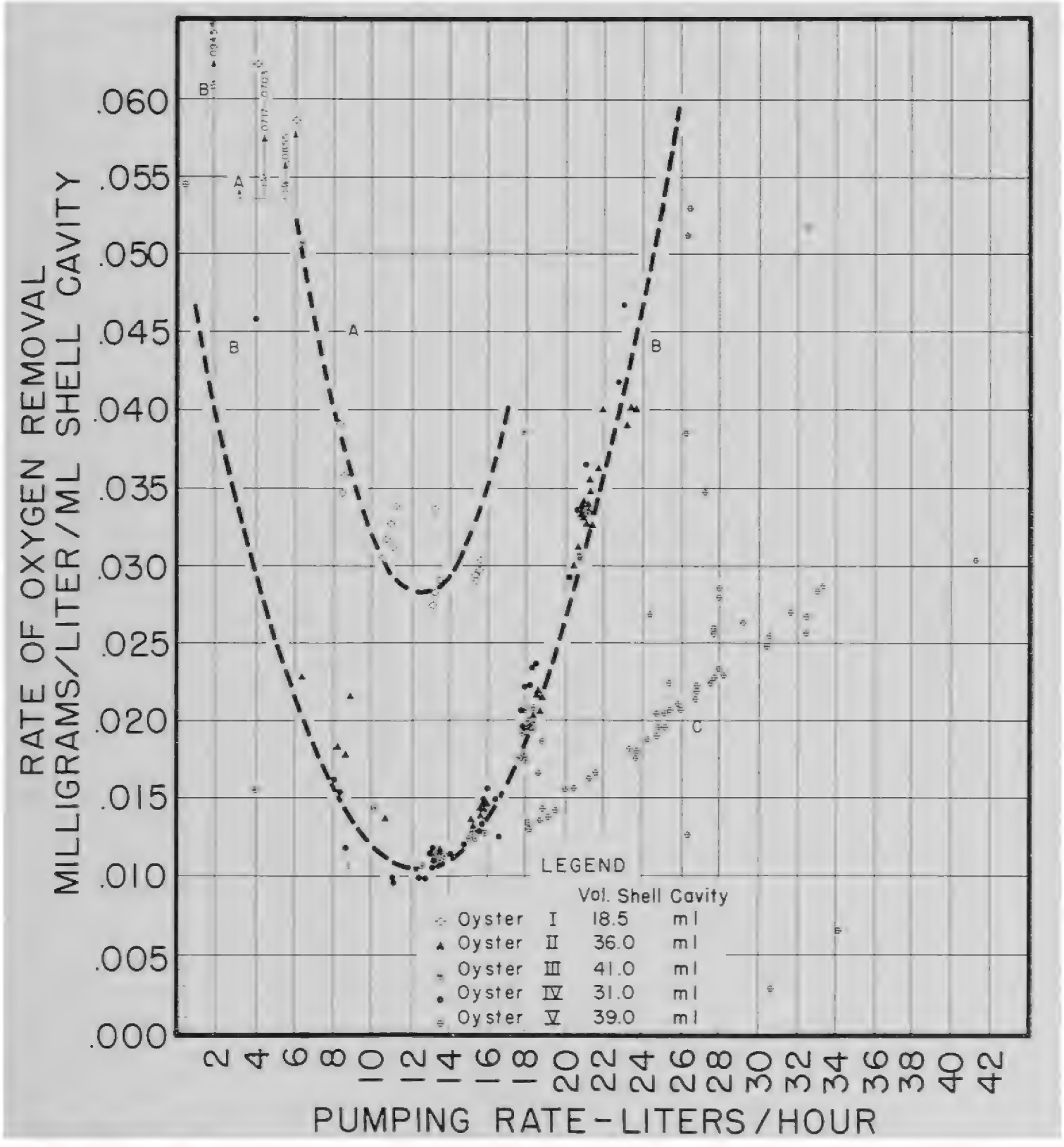

Fig. 1. Rate of oxygen removal by oysters, milligrams of oxygen removed per liter per milliliter of shell cavity plotted against pumping rate. To obtain hourly oxygen utilization, multiply values on ordinates by total volume of shell cavity times desired pumping rate.

actually increases as the curve approaches the minimum because the increased volume of water more than makes up for the decreased rate of removal of oxygen per unit of water (Figure 2). At a point between 12 and 13 liters per hour the rate of removal of oxygen per unit of water pumped begins to increase with increased pumping rates, and the right limb of the parabola is formed. This limb represents the pumping rates characterized as Phase III pumping and is characteristic of an actively pumping oyster. The 12 liter

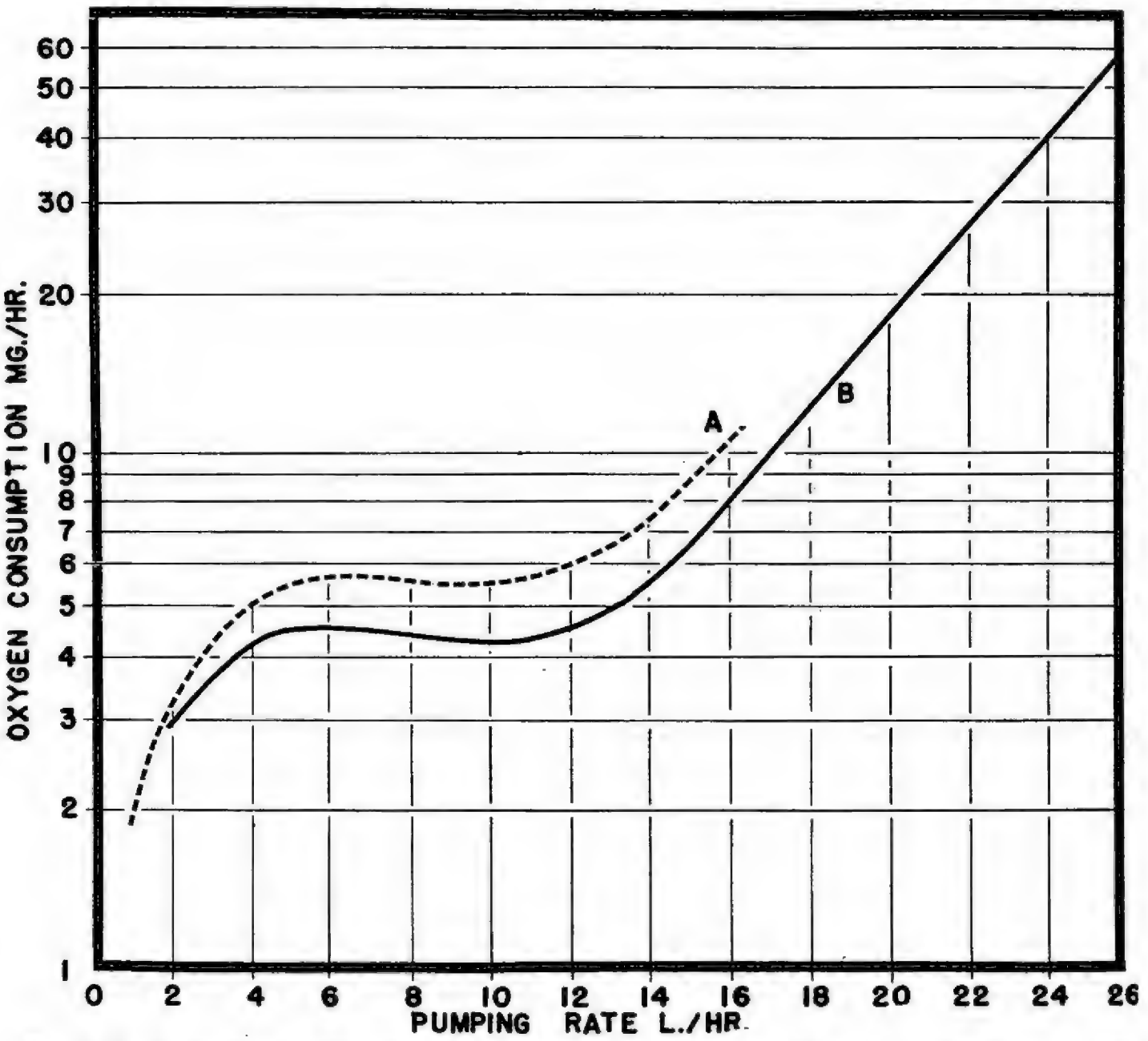

FIG. 2. Total oxygen consumption of oysters pumping at various rates. "A" is for oysters of 18 ml shell cavity and "B" is for oysters of 36 ml shell cavity. Curves derived from Figure 1.

per hour point is at the maximum pumping rate of the testing period and since the oxygen uptake is low this may represent the rate at which the oyster can circulate water through a minimum portion of the branchial system with a minimum of work. Above this, the total oxygen consumption may reach 40 mg per hour for an oyster with a shell cavity of 36 ml (about a three inch oyster) at a pumping rate of 24 liters per hour (Figure 2).

The curve for the rate of oxygen removal from the water for a small oyster is shown by curve A, Figure 1. Although there are insufficient observations to completely resolve the curve, it is clear that the smaller animal has a higher rate of intake per unit size than the larger one, an observation consistent with general knowledge concerning respiration. The parabolic relationship is suggested in this case because of the similar case for the larger oysters.

The loci of the parabolas, shown as dashed lines through the points, were approximated empirically and are expressed by the following equations:

$$\text{For curve A } y = \frac{(x - 12.4)^2 + 45.6}{1627}$$

$$\text{For curve B } y = \frac{(x - 12.4)^2 + 38.4}{3661}$$

where x = pumping rate in liters per hour and y = rate of oxygen removal from the water in mg/liter/ml shell cavity.

The results obtained from one oyster to the next were not as precise as these equations infer. Curve C, in Figure 1, illustrates this point. There is no information which will satisfactorily explain this type of respiratory behavior, although it is to be remembered that these observations were made over a period of some months and the variations could represent some metabolic change in the oyster during that time. Even so, the total uptake for this oyster during Phase III pumping rates was much more than the values of Mitchell 1914 and Galtsoff and Whipple 1931 and while pumping at 32 liters per hour it utilized approximately 37 mg of oxygen per hour. In view of the relatively low oxygen requirements reported by other workers, these large values require an examination of their significance in terms of nutritional requirements and work output.

Discussion

Work and Pumping Efficiencies

The principal difference between our results and those reported by other workers is that the oxygen uptake was measured while the oyster was doing measurable work. Jørgensen (1952) attempted this using the method of Fox (1937). This permitted measurement of pumping rates up to 16 liters per hour, slightly beyond the 12.4 liter per hour transitional point mentioned above. As a result, it is impossible to compare values simply in terms of oxygen uptake. The constants for computing the data used in the discussion of the next few paragraphs are listed in Table 1.

Table 1
Data for computations

1 ml oxygen (STP) weight 1.43 mg
1 joule = 10^7 ergs
1 calorie = 4.185 joules
1 mg carbohydrate = 4.1 calories
1 mg oxygen equivalent to 1.17 mg carbohydrates
1 mg oxygen yields 3.5 calories in combining with carbohydrate
1 gram = 980 dynes
Mean density of sea water pumped by oysters = 1.015 gm/ml
1 ml sea water, mass 1.015 gm/ml weighs 995.38 dynes.

In Figure 3 the rate of oxygen consumption (illustrated in Figure 1) has been converted to work done in joules for the various pumping rates, B-B′. For comparison, the theoretical curve for the transfer of potential energy required to move similar volumes of water is also plotted, A-A′. The latter is calculated according to Jørgensen (1955) from the relationship:

ml pumped times pressure in cm times weight of 1 cm in dynes/cm^2 = work in ergs.

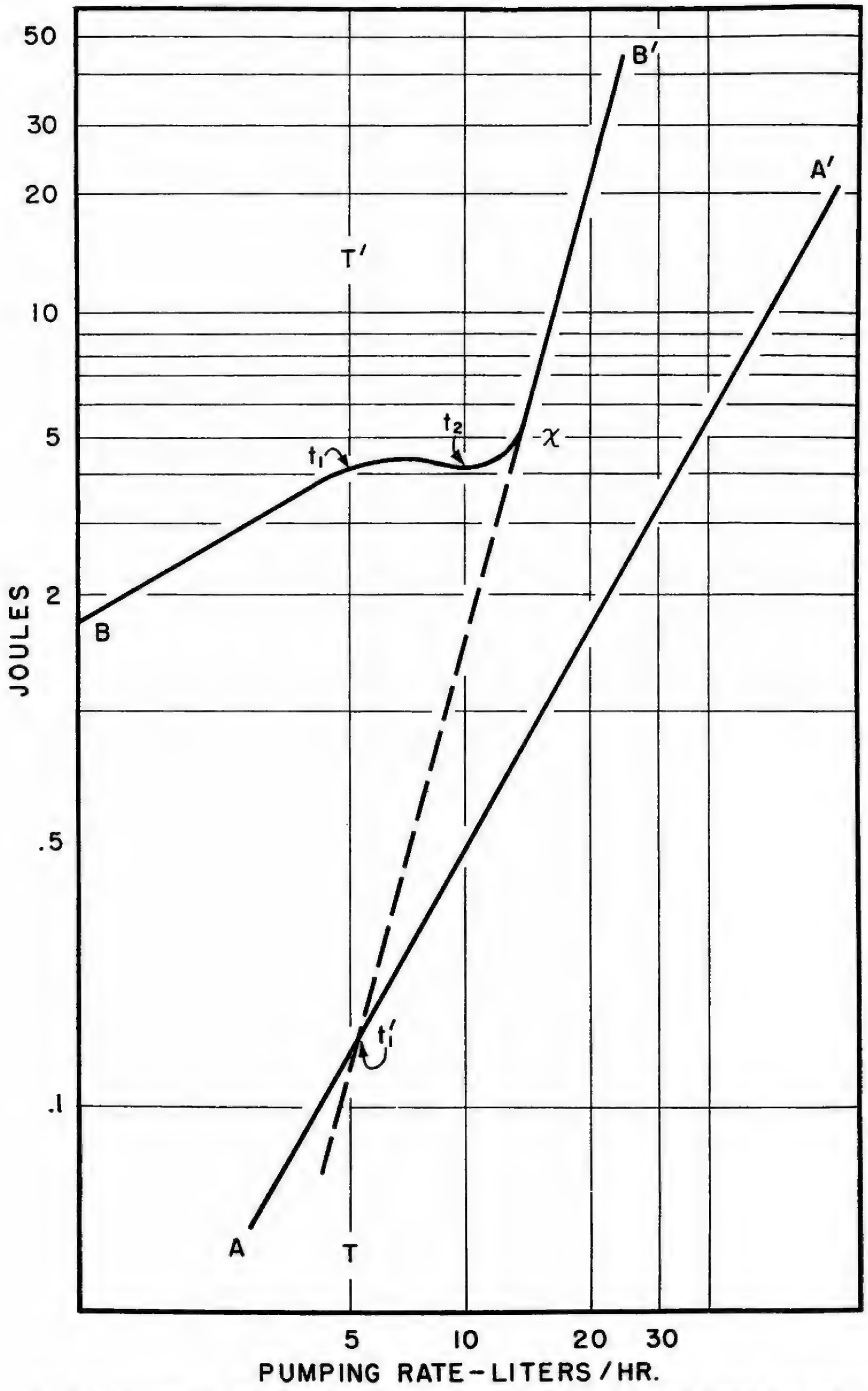

FIG. 3. Comparison of work done at various pumping rates as calculated from oxygen uptake with theoretical requirements (without internal resistance, etc.). B-B′ curve computed from oxygen uptake values derived from parabolic relationship shown in Figure 1. A-A′ theoretical work required for pumping rates indicated (Based on equation given by Jørgensen, 1955).

The form of B-B′ is determined by the parabolic nature of the primary oxygen uptake curve. That part of the curve to the left of the 12 liter/hr. intersect comes from the left limb of the parabola and that to the right from the right limb. It is clear that the two limbs concern two entirely different aspects of oyster respiratory behavior. That part of the curve B-B′ up to t_1, as mentioned earlier, represents the recovery from the oxygen debt incurred during closure. The region t_1–t_2 encompasses the range of pumping rates which has been designated as Phase II (testing period). Our interpretation here is that from 5 to 10 liters per hour can be pumped with little difference in oxygen uptake, with the differences in volume varying according to the amount of ciliated tissue involved in actual pumping. It is possible that the oxygen uptake during this interval approximates that of the basal metabolism of the animal. At any rate, the benefits accrued from the water pumped within this range are gained by a minimum expenditure of energy.

If the right extension of the curve is extended from the inflection X to where it intersects A-A′ at t'_1 we can fix the point at which pumping would theoretically be 100 per cent efficient. It may be more than coincidence that this point is nearly at the five liter per hour level and corresponds to t_1 on curve B-B′. In other words, beyond t_2 all cilia available for pumping are at work and the inefficiency of the ciliated epithelium comes into play. As in other power-work systems, efficiency decreases as the rate of work output increases beyond a certain critical point. For these oysters, the efficiency at 10 liters per hour is 10 per cent, at 25 liters per hour it is five per cent. By extrapolation we would expect the ciliated epithelium of an oyster pumping at 40 liters per hour to be about 1.5 per cent efficient. The latter is in close agreement with Ludwig's (1931) estimate of two per cent for the individual ciliated cell but my value for 10 liters per hour is not. One and five tenths (1.5) per cent is approaching zero efficiency and is probably indicative that 40 liters per hour is near the maximum pumping capacity of the animals in this size range. Larger animals could pump greater quantities of water but they would also require greater amounts of oxygen.

In computing the values for A-A′, I used a pressure range of 0.1 cm at one liter per hour to 0.9 cm at 25 liters per hour. These were interpolated from my observation that an oyster pumping at approximately 40 liters per hour produces a one cm hydrostatic head. This is consistent with Nelson's (1936) observation of 0.7 cm at 16 liters per hour.

Relationships Between Oxygen Uptake, Energy Requirements, and Available Food

Adequate data on the caloric values of suspended and dissolved organic materials are not available. However, some useful information can be derived from the literature indirectly by examining data for types of organisms which may serve as oyster food. *Nitschia closterium* is representative of the size of some of the smaller phytoplankton organisms and *Prorocentrum* is a typical member of the flagellate flora of the marshes and is somewhat larger. The contribution that these organisms can make towards meeting the caloric requirements of the oyster will be compared in the following paragraphs.

The dry weight of *N. closterium* is given by Ketchum and Redfield (1949) as 2.32×10^{-11} grams per cell. These organisms were from laboratory cultures and may not be typical. Also, the species may not be as large as many organisms available to the oyster as food. Based on other material from Ketchum and Redfield (1949) the average composition of algae can be approximated as: protein 45%; carbohydrate 30%; and

lipids 25%. Unfortunately, no data are available on the caloric values of these materials as they occur in plankton, but from Hawk, Oser, and Summerson (1947) we have the following: mixed plant and animal protein 4.1 large calories per gram, carbohydrates 4.1 large calories per gram, and fats 9.3 large calories per gram. For the present application these figures will aid us in getting the overall picture, although it is realized that some revision will be in order as more experimental results become available. The computations to be explained are summarized in Table 2.

TABLE 2

Postulated composition and energy content of *Nitschia* type cells
(Postulated dry weight of 10^6 cells 0.02 mg. Such cells as *Isochrysis galbana* are similar in size)

Food class	Percent	mg/10^6 cells	cal*/mg	cal*/10^6 cells
Protein	45	.009	4.1	0.0369
Carbohydrate	45	.006	4.1	0.0246
Lipids	25	*.005*	9.3	*0.0465*
Totals		.020		0.1080

* Note that these units are *small* calories.

Bainbridge (1957) has reviewed the literature on phytoplankton concentrations and from this we can judge that a range of 0 to 10 million cells per liter would be reasonable for inland waters although μ-flagellates are reported in much greater concentration (Droop, 1954). This then gives us an estimate of up to 1.08 calories available per liter of water if all the organisms are similar to *N. closterium* in size.

Let us assume that the basal metabolism of the oyster is indicated by the oxygen uptake during the testing period. At a pumping rate of 10 liters per hour, 4.4 mg O_2 per hours is consumed. At 10 liters per hour and a concentration of 10^6 cells per liter of *N. closterium* 1.080 calories could be acquired, assuming for the moment 100 per cent filtration and assimilation. An uptake of 4.4 mg O_2 represents 15.4 calories or 14.3 more than available in the phytoplankton present. If these oxygen consumption values are even approximately correct it is clear that the animal is either using a reserve of stored energy or is capable of utilizing dissolved organic materials directly from the water, or else the *Nitschia* type of food is not adequate except in unlikely concentrations. Even at 12×10^6 cells per liter the caloric value just barely matches the 10 liter per hour expenditure of energy by the oyster.

The dinoflagellate genus *Prorocentrum* is a common organism in the marsh and estuarine plankton. Collier (1958) published data relative to its carbohydrate content and its production of non-particulate carbohydrate in laboratory cultures. Although it is not presumed that these data are applicable to field conditions, they will be useful in discussing the problem at hand.

The cell volume of this organism is estimated at 104 cubic microns. This amounts to 10^{-2} $cm^3/10^6$ cells, and using 25 per cent as a median value from the estimates of Ketchum and Redfield (1949) for solids, we find a dry weight of approximately 2.5 mg/10^6 cells. Using the same food-class composition as applied in the case of *Nitschia* we derive the caloric value of *Prorocentrum* as shown in Table 3.

One million cells provide an estimated 13.6 calories which is about 125 times the value for *N. closterium*. Since there are no estimates on the caloric values based on actual calorimetry this difference is due solely to volume of cells. It is interesting to

TABLE 3

Postulated food-class composition and energy vaule of *Prorocentrum* type cell

Food class	Percent dry weight	mg/10^6 cells	cal*/mg	cal*/10^6 cells
Protein	45	1.13	4.1	4.663
Carbohydrates	30	0.75	4.1	3.075
Lipid	25	0.63	9.3	5.859
Totals		2.51		13.597

* Note that these units are *small* calories.

note that an estimate of 0.75 mg carbohydrate/10^6 cells based on the 25 per cent value arbitrarily selected from the data of Ketchum and Redfield differs only by 0.55 mg measured by the N-ethylcarbazole method (Collier, 1958).

If 10 liters of water containing 10^6 cells per liter of this organism were filtered, the total yield could be as much as 135 calories or almost nine times the caloric equivalent of the 4.4 mg O_2 uptake.

Beyond this minimal phase of oxygen uptake, beginning at about 12 liters per hour, the increase in oxygen consumption with increased pumping rate is very rapid. At the 24 liter per hour level the caloric equivalent would be approximately 150 calories per hour. A population of *Nitschia* of 12×10^6 cells per liter being filtered at 24 liters per hour could provide a maximum of only 35.0 calories. However, at this pumping rate, a concentration of only 10^6 cells per liter of *Prorocentrum* would supply about 350 calories. In the latter case there would be no problem of the oyster using more energy to pump than it can take from the water. The concentrations indicated, therefore, seem reasonable, particularly when it is considered that other types of cells are usually present and contribute to the total nutritional value of the water.

Another phase of the relationship between the oyster's pumping activity and the organic content of the water pumped involves a possible sensory stimulation by non-particulate carbohydrates. This was reported in some detail by Collier *et al.* (1953). After making successive hourly observations (day and night) for over 18 consecutive months, it was found that pumping responded directly and quantitatively to substances whose concentration could be estimated by the N-ethyl-carbazole reagent for carbohydrates. The evidence suggested that these materials were at least in part dissolved and were produced by microorganisms. If their concentration was not above certain thresholds when the oyster opened for testing the water the oyster closed. If the concentration was sufficiently high, pumping continued at a rate which thereafter fluctuated according to changes in the carbohydrate concentration.

Such a mechanism could have high survival value for the species. Immobile filter feeders are dependent on what the water circulation brings to them. Continual filtration would soon use up all energy reserves. (A fat oyster three inches in length with a six per cent glycogen content pumping at 10 liters per hour would burn all of its reserve in about 400 hours if there were no replenishment.) Random filtration would provide only a moderate improvement. This mechanism enables the oyster to test the water and pump when the likelihood of obtaining food is greatest.

This stimulating function of the dissolved materials, whatever they may be, is not necessarily their only significance. If the basal metabolism maintains a level at which five mg of O_2 per hours is consumed, the carbohydrate equivalent would be 4.3 mg of

carbohydrate on combustion. The combustion equivalents of carbohydrate would be on the order of 35 to 40 mg per hour at the higher levels of pumping rates. A series of determinations of the rate of removal of carbohydrate from the water pumped by a single oyster were made to learn if the quantities actually removed were significant. The results are shown in Figure 4. The actual observations are indicated as points in the scatter diagram and the theoretical amount of carbohydrate required for the various oxygen consumptions (shown in Figure 1) are represented by the curve about which the points are scattered. The agreement of the points with the curve is surprising. Since this makes it appear that the oyster actually removes carbohydrates from the water at rates commensurate with the energy requirements of the work done in pumping water, these and related questions must be answered: (1) Can the animal automatically adjust its pumping rate to the level of energy available in the water? (2) Are the ciliated cells

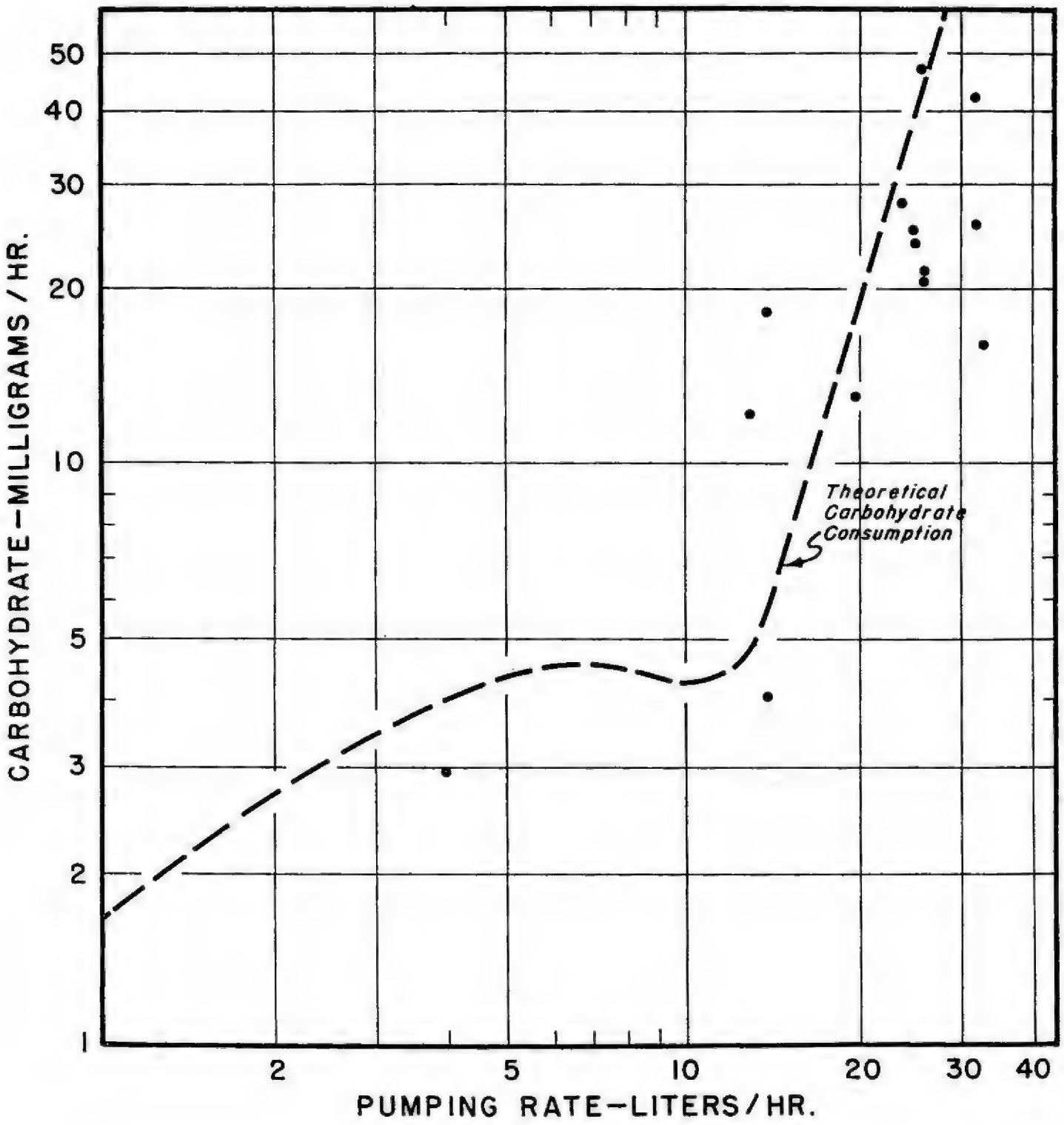

FIG. 4. Carbohydrate consumption for various pumping rates derived from oxygen uptake curve of Figure 1. Dots represent actual observations on carbohydrate removed from water by oyster at pumping rates indicated.

capable of utilizing dissolved materials directly from the water? (3) Is there another explanation? The available data are insufficient to resolve these problems but additional effort would be justified.

Jørgensen (1955, p. 423) may have generalized too broadly in indicating that Collier, Ray, and Magnitzky (1950) and Wangersky (1952) reported up to 100 mg of carbohydrate per liter for all sea water and in indicating that one mg removed for each liter of water pumped is several times the food requirement of oysters. Up to 100 mg of material per liter was found in some rich marsh waters and a concentration of dense plankton from a red tide outbreak yielded values of 50 mg per liter. However, as shown in the report of 1953 (Collier *et al.*), the Gulf of Mexico waters are generally poor in carbohydrates while the estuaries are comparatively rich. The results reported on oxygen uptake in this paper would indicate that the oyster has a high energy requirement when pumping at maximum rates and that the amount of carbohydrate removed is consistent with this.

Guillard and Wangersky (1958) published an account of some experiments designed to demonstrate the relationship between concentrations of algal cells in artificial cultures and the accumulation of extracellular carbohydrates in the culture medium. They concluded that ". . . carbohydrate production in cell-free medium did not parallel cell numbers in cultures of any of the organisms studied. Such accumulation as occurred began with the end of the logarithmic phase of growth, and in most instances, increased during the stationary phase or senescence of the cultures. The fact that killing cells liberates comparatively large amounts of carbohydrate supports the idea that its presence, particularly during the phase of actual growth, is due largely to the death of the cells."

These statements contain the premises on which the authors, in speaking of natural populations, base the additional conclusion that "assuming that these organisms behave like stationary cultures the maximum amount of carbohydrate liberated would not exceed one mg/L." They pointed out that the relative sizes of organisms were not considered.

When the cell counts of Guillard and Wangersky (1958) are converted to mg dry weight/l and plotted with extracellular carbohydrates in mg/l against time on semi-log paper, it is seen that an interpretation different from theirs is possible.

Using an estimated volume of 72 cubic microns for *Monchrysis lutheri* and applying the same constants as used for the other organisms in an earlier section of this paper, we can estimate the dry weight at about 0.018 mg/10^6 cells. Applying these factors to Guillard and Wangersky's data and plotting as described above, Figure 5 is obtained. This method of graphing reveals a definite tendency of extracellular carbohydrates to increase with the growth of the culture, even during the log phase. The tendency is even more clear in the case of *Prymnesium parvum*. The fact that my estimates of cell volume for these organisms may be in error would change the positions of the curves but not their slopes.

A point of special interest is the curve for carbohydrate production per mg of cells. Apparently the cells are producing carbohydrate at a declining rate during the logarithmic phase but, nevertheless, they are producing it. The total carbohydrate increases because cell multiplication more than compensates for the decreased rate of production per unit of cells. It is noticed that the minimum rate of carbohydrate production coincides with the termination of the logarithmic phase.

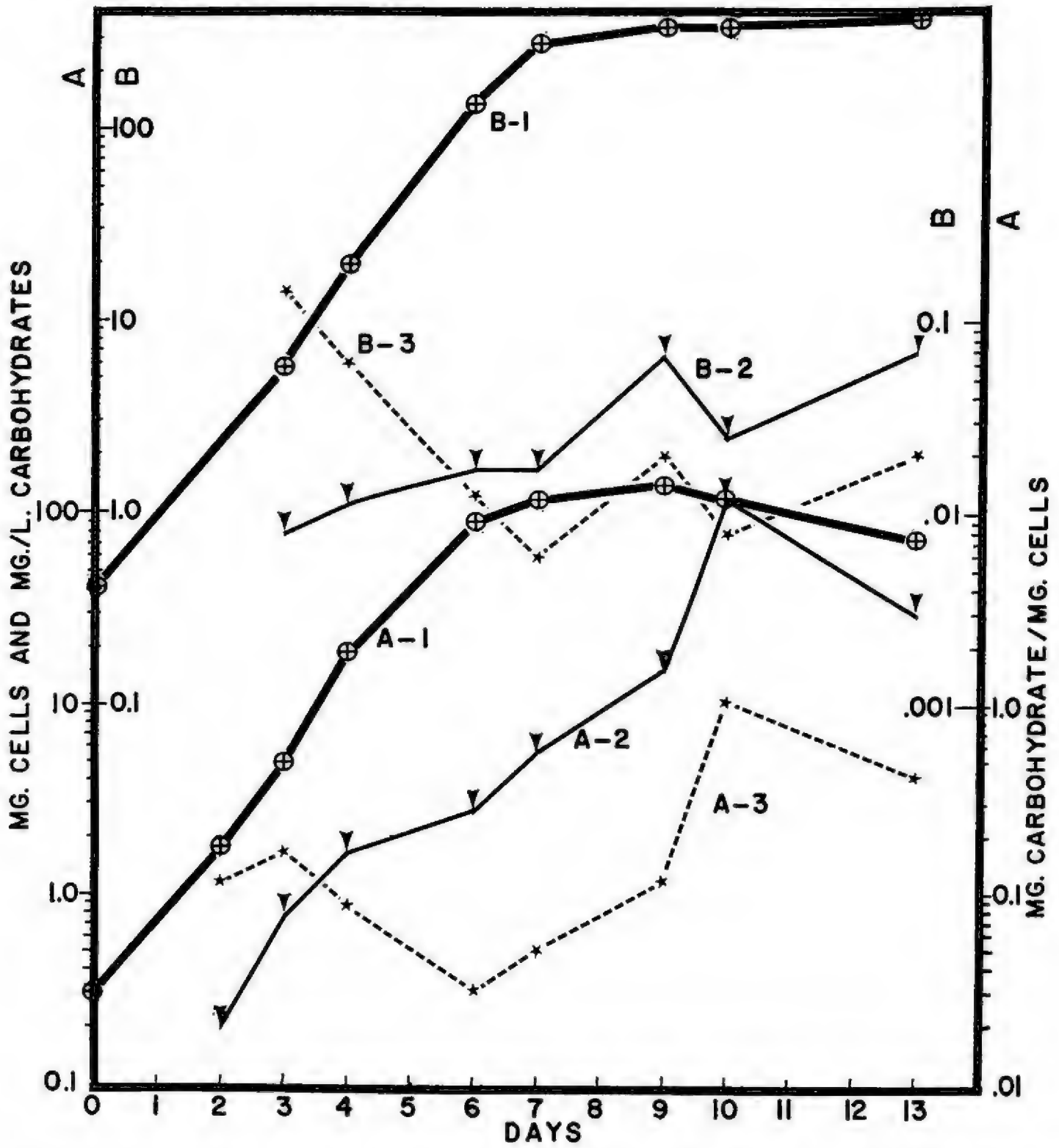

FIG. 5. Production of extracellular carbohydrates by unicellular algae. For *Prymnesium paruvim* "A-1" represents growth rate of algae in mg dry weight. "A-2" is the rate of accumulation of total extracellular carbohydrate as mg/l and "A-3" is the rate of production of carbohydrate per mg of cells (dry weight). For *Monochrysis luthuri* "B-1," "B-2," and "B-3" are respectively the same as "A-1," "A-2," and "A-3" above. Data from Guillard and Wangersky, 1958, p. 452, Table 1.

Since the oyster may be able to regulate its pumping activity according to the food content of the water, these points may become pertinent. In addition, it is conceivable that the "free" carbohydrates could be used as an energy source directly by the ciliated epithelium. Thus, they would be useful to the animal as a means of conserving energy if their abundance were related to the algal concentration.

Summary

1. Several workers have studied oyster respiration (Mitchell, 1914, Galtsoff and Whipple, 1931, and Jørgensen, 1952), but none of these have measured oxygen uptake over the full range of pumping rates of which the oyster is capable.

2. A modified Winkler method using the syringe pipette of Krogh (1935) was adopted for the determination of dissolved oxygen. Reagents were modified according to Pomeroy and Kirshman (1945).

Oxygen uptake by the oyster was determined by difference between inhalant and exhalent water. The experimental arrangement of the oysters was a combination of the rubber dam method and the constant level tank as described by Collier and Ray (1948) and Collier *et al.* (1953).

3. Shell cavity volume in ml was used as a common denominator for reduction of the data because of differences in size of oysters and possible changes in glycogen content over long periods of observation.

4. "Pumping rate" is used to designate the rate at which the oyster moves water through its branchial systems to avoid the ambiguities of "filtration rate" or "feeding rate."

5. The oyster exhibits three different phases of gape (or degrees of openness) of valves, each characterized by a magnitude of pumping rate. These phases must be included in a consideration of respiration.

6. Analysis of oxygen uptake data in terms of pumping rates yielded parabolic curves, with the minimal uptake in each case occurring at a pumping rate between 12 and 13 liters per hour. Beyond this point the uptake increased to its maximum very rapidly. A three inch oyster pumping at a rate of 24 liters/hr. may consume 40 mg of O_2 per hour.

7. A comparison of oxygen uptake and work performed in pumping water suggests a maximum efficiency during Phase II pumping (the testing phase). A theoretical efficiency of one to two per cent at maximum pumping rates is deduced.

8. By theoretical considerations, the caloric value of different types of plankton organisms are compared to the energy demand of the oyster in terms of oxygen uptake. It is found that high concentrations of cells of the *Nitschia* type could not provide sufficient energy to balance that expended in pumping, even with 100 per cent utilization, while cells of the *Prorocentrum* type could easily provide adequate energy.

9. It is suggested that extracellular carbohydrate (as reported by Collier *et al.*, 1953) could supply a directly available source of energy for the ciliated epithelium in pumping water and at the same time provide a means for the oyster to regulate its pumping according to the concentration of derivable plankton elements. It is possible that the necessary sensory mechanism for accomplishing this exists.

10. The data of Guillard and Wangersky (1958) suggests that extracellular carbohydrates are produced in a manner related to the numbers of cells in a population of algae, although these authors conclude that such is not likely.

11. Also from the data of Guillard and Wangersky (1958), it is found that the rate of carbohydrate production per unit of cells diminishes as the logarithm phase progresses, but the decrease is more than compensated for by the increasing number of cells. The net result is an increasing amount of extracellular carbohydrates during the logarithmic phase of cell growth.

12. It is believed that the problem of extracellular carbohydrates is of greatest importance in the study of oyster nutrition.

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Standing Crop, Chlorophyll Content and *in Situ* Metabolism of a Giant Kelp Community in Southern California[1]

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Abstract

Fresh wet standing crop, chlorophyll "A" content, and total metabolism of a giant kelp community, *Macrocystis pyrifera* were investigated during early summer at Paradise Cove, California. Standing crop varied from 4.35 to 5.78 kg/m^2, while chlorophyll "A" varied from 0.69 to 0.92 gm/m^2. Highest values occurred toward the center of the kelp bed. Gross photosynthesis (Pg) balanced respiration (R) obtained from measurements of oxygen (R = 33–37 gm O_2/m^2/day; P_g = 31–36 gm O_2/m^2/day). The magnitudes of standing crop, chlorophyll "A" content, and metabolism indicate that giant kelp has a productive capacity similar to other highly productive ecosystems like coral reefs, some springs, and marine grass flats.

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[2] Contribution No. 13, Marineland of the Pacific Biological Laboratory.

Introduction

The giant kelp communities of *Macrocystis*, found along the North and South Pacific coasts of the western hemisphere and at various localities between 40° and 60° south latitude (Gessner, 1955), represent one of the dominant plant communities of sublittoral temperate, boreal, and austral seas. These aquatic "forests" envelope a rich biota of other plants, invertebrates, and fishes all mingled in intricate complexity. The kelp communities of southern and Baja California have been the subject of ecological research by the Kelp Investigations Program at the Scripps Institution of Oceanography since 1956. However, as yet no data have been provided that allow comparison of the productive potential of a kelp community with other aquatic ecosystems such as coral reefs, lakes, etc. This paper reports data on standing crop, chlorophyll content, and *in situ* metabolism of a giant kelp community that allows comparisons to be made with other ecosystems studied in a similar manner.

Acknowledgments

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Description of the Area Studied

This investigation is confined primarily to a rather dense but shallow stand of the kelp, *Macrocystis pyrifera* (L.) located in Paradise Cove, California, at the Northwest end of Santa Monica Bay[3] (Figure 1). During 1957 and 1958 kelp beds in the southern California region suffered severe damage (North, 1957b). Reduction in the surface canopies was extensive. North has correlated the reduction with the unusually high summer water temperatures that have prevailed in this region in the last few years. The kelp beds at Paradise Cove apparently have not been subject to as severe damage as other beds in southern California, although North (1958, personal communication of Dr. Michael Neushul) did observe temperature damage and black rot in the canopies of the region. During the months of May, June, and July, 1959 (the period of this study) the Paradise Cove beds were luxuriant and showed no evidence of heat damage and very little presence of black rot on the fronds.

Studies were carried out at stations indicated in Figure 1 in depths of approximately

[3] Extensive work has been done on *Macrocystis* in the area by Dr. Michael Neushul, including nomenclatorial considerations that remain unpublished. ("Studies on the Growth and Reproduction of the Giant Kelp, Macrocystis," Ph-D dissertation, University of California, Los Angeles, June 1959).

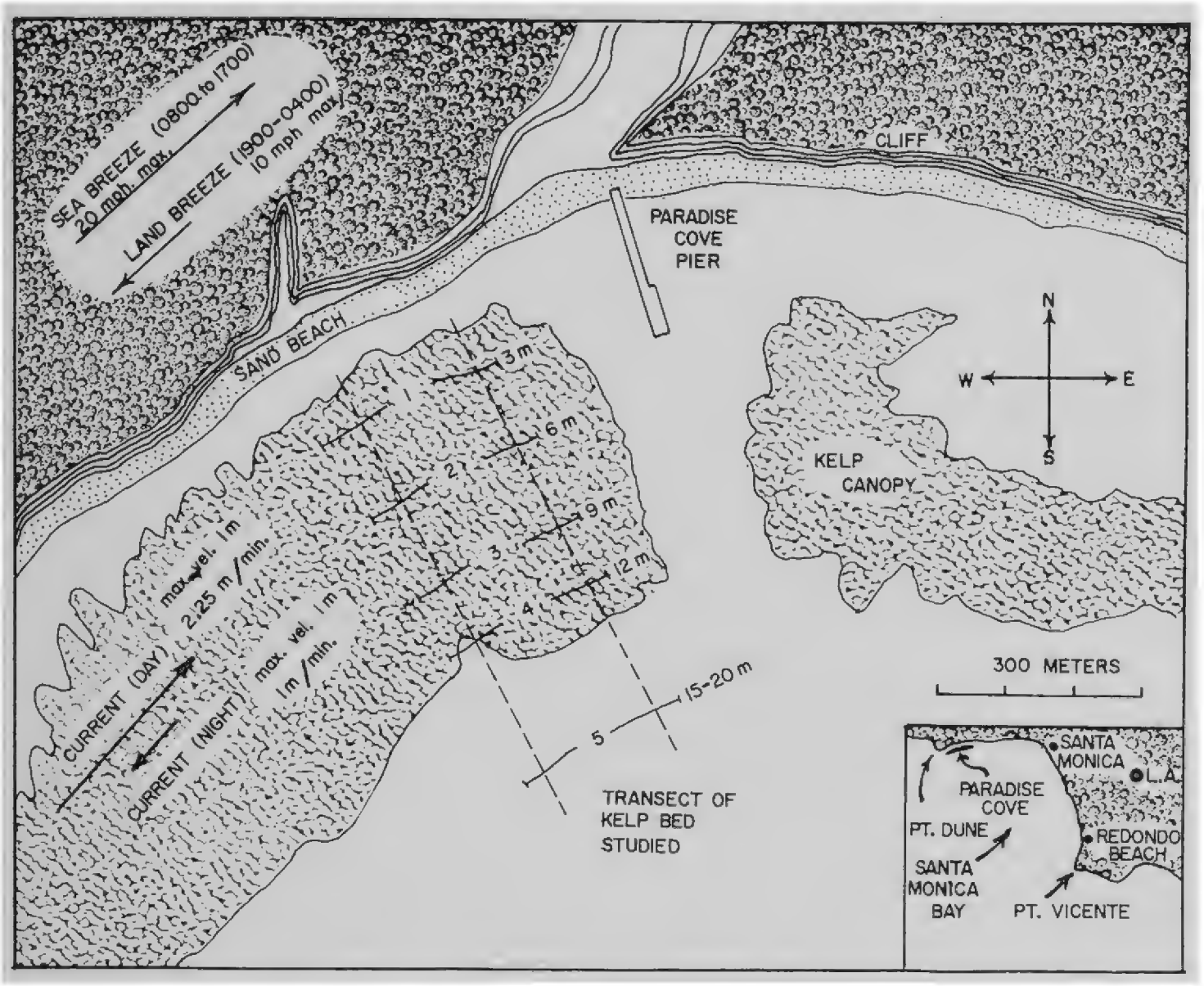

FIG. 1. Diagrammatic map of the kelp beds of *Macrocystis pyrifera* investigated at Paradise Cove, California. The numbers one through five indicate sampling stations at various depths within and outside the kelp community.

3, 6, 9, and 12 meters within the kelp bed and outside the bed in water 15 to 20 meters deep. When the stations were set up the tidal range was 5.7 feet and tides oscillated only above the zero tidal mark. The stations were established when the tidal level was approximately + 2.9 feet and at the mid-point of its tidal range. During the period of study, therefore, water level tended to oscillate both above and below the depths indicated in Figure 1. Examination of the bed in the shallower areas was accomplished with a diving compressor and Desco mask, while aqua-lungs were used in the deeper portions of the bed.

SUBSTRATE CONFIGURATION IN THE KELP BED

Coursing out from the cliffs surrounding the cove and almost perpendicular to the beach at 100 to 200 foot intervals are a series of dense, fine-grained rock ridges. The bottom between these ridges consists of a semi-lithified mud upon which most of the kelp holdfasts are attached. This mud is covered with varying amounts of beach sand that in places creates a pure sand bottom several inches deep. Cobbled areas of small stones and shells and occasional rocks also occur between the ridges.

The kelp plants grow in this area at depths from about three meters on the inshore side to a maximum depth of about 12 meters on the outside of the bed and, therefore, represent a shallow bed since *Macrocystis* often occurs in depth to 20–25 meters. Mature kelp plants were not found growing on the rock ridges, probably due to the

presence of large numbers of the sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* which are known to be predatory on *Macrocystis* and other algae (Andrews, 1945; North, 1957a; North, 1958). In fact, the presence of underlying rock ridges populated with sea urchins could be detected from the surface by open-water paths through the bed that were devoid of canopy.

Currents

Current velocity and direction in the kelp bed were determined at the surface and at one meter below the surface using fluorescein dye as an indicator at Stations of 3, 6, and 9 meters depth (stations I, II, and III, Figure 1). Measurements were made at three hour intervals during two 24 hour periods on June 13–14 and July 2–3, 1959. The direction of water current through the bed was found to be related directly to the direction of prevailing winds, while current velocity was proportional to the wind stress. The Paradise Cove area, like the entire Santa Monica Bay region, is normally subject to strong daily land-sea breezes during summer months. At Paradise Cove, the mornings are characterized by gentle sea breezes from the southwest (less than two mph) which increase gradually during the afternoon to a velocity of 15–20 mph. In the late afternoon (1700 hr.) the wind shifts rapidly from the southwest to the northwest and by 2000 hr. is a land breeze from the northeast with moderate velocity (10 mph, see Figure 1). This land breeze diminishes in intensity through the night and is again replaced in the morning, without noticeable wind shifts, by the gentle sea breeze. Currents at the surface and one meter below the surface reacted rapidly to the changes in wind direction and velocity.

Generally, surface velocities were three to four times higher than current velocities at one meter depth. In addition, water velocities increased progressively from the inside to the outside of the bed (from stations I and II to III, Figure 1), but seldom deviated by more than two fold. Maximum velocities attained at the surface were from 3 to 6 meters/min. in the late afternoon (1600 to 1700 hr.). Maximum velocities one meter below the surface were 1.5 to 2.25 meters/min.

Although currents course through the bed in opposite directions during the period of one day, there is a net movement of water through the bed in a northeast direction (Figure 1). Direction of the currents could also be detected by the bending of kelp fronds in the direction of the current.

On June 3, 1959, the first day that samples were collected by diving, a feeble surge was noted on the bottom at a depth of three and six meters. On June 4 and everyday that diving was performed through June 16, a strong surge prevailed on the bottom at depths of three to six meters and to a lesser extent at nine meters. Considerable surge was apparent from the surface to the bottom at three meters depth but only from one to two meters above the bottom in deeper areas of the bed. The surge was effective in transporting large amounts of sand and detritus and this considerably reduced visibility. Although oscillation of transported materials was noticeable, a net transport outward along the bottom of the kelp bed was observable at all times during periods of heavy surge. In the inner margin of the kelp bed (three meters) diving had to be abandoned completely after the second day because of excessive surge and poor visibility.

Light Penetration

White light absorption was measured at various depths using a submarine photometer. Values obtained at various times of the day within the kelp bed indicate that the per cent absorption is slightly greater (about 20 per cent on the average) at any given depth than outside the canopy (Figure 2), but the extinction coefficients are similar. Since the photometer was purposely lowered between plants in areas where it was visible from the surface, the slightly lower values probably indicate the absorption of scattered light by adjacent kelp fronds. Examination of the extinction coefficients (slope of the various lines) indicate that at approximately two to three meters above the bottom absorption increases considerably in six and nine meters depth as compared to greater depths, whereas in four meters depth, absorption was quite high from just beneath the surface to the bottom. The turbidity results from the heavy surge that prevailed in the area (see previous section).

Maximum white light intensity was attained between 1100 and 1400 hr. at all depths. However, maximum values outside the kelp bed tended to be shifted toward the early

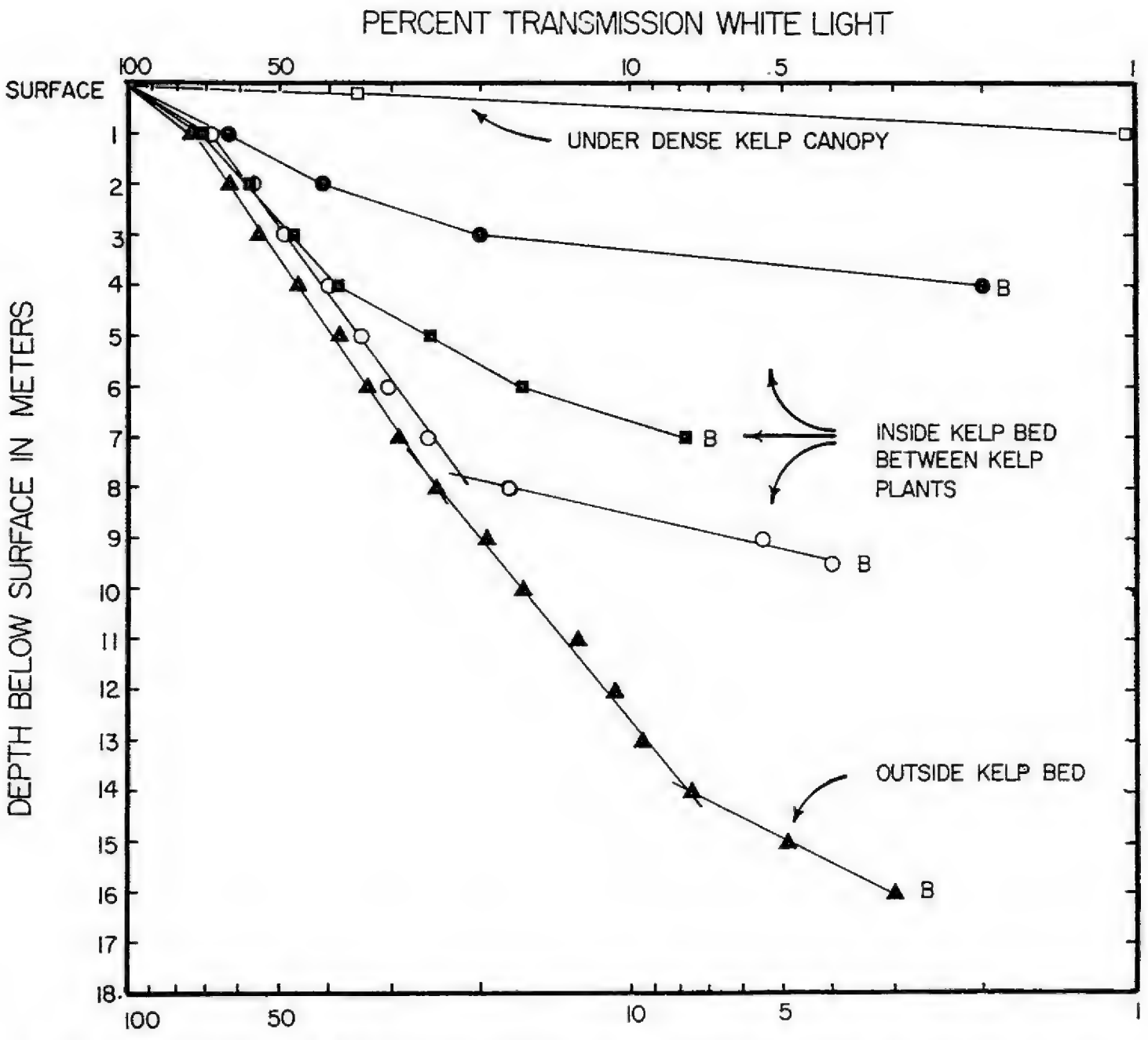

Fig. 2. Light transmission as a function of depth both inside and outside the kelp bed at Paradise Cove, California. The end of each line indicates the bottom depth with the exception of the surface canopy line (open squares). Note the sharp increase in absorption of light approximately two to three meters above the bottom.

afternoon below three meters depth, while within the kelp bed they were shifted toward the late morning (Figure 3). The shift within the bed is the result of kelp orientation, the kelp effecting a greater degree of shading in the afternoon.

In studying light quality beneath kelp canopies Neushul (1957) found that one blade thickness absorbed approximately one-third of the incident green light and that subsurface illumination beneath the canopy was from 0.9 to 1.1 per cent of the incident illumination. Measurements made under kelp canopies in this study support this conclusion. In areas with thick canopies 40 to 50 per cent subsurface transmission was recorded for white light at 5 to 6 cm depth, whereas zero per cent transmission was recorded at one meter depth just below the canopy (Figure 2). On two occasions surface kelp blades were placed directly over the photometer and transmission recorded. Values were almost identical and were averaged, one blade 36%, two blades 14%, three blades 5%, four blades 2.4%, five blades 0.8%, and six blades 0.0%. Each blade, therefore, absorbed about two-thirds of the incident white light.

Neushul (1957) states that beneath the canopy, "The undergrowth rarely exceeds two meters in height, and the bottom community is frequently quite open. Thus the main light-modifying layer of vegetation is the surface canopy." At Paradise Cove undergrowth within the kelp bed never exceeded two meters in height and more often was less than one meter. These results certainly support Neushul's statement that, "Light is apparently one of the chief factors determining the structure and components of the kelp bed."

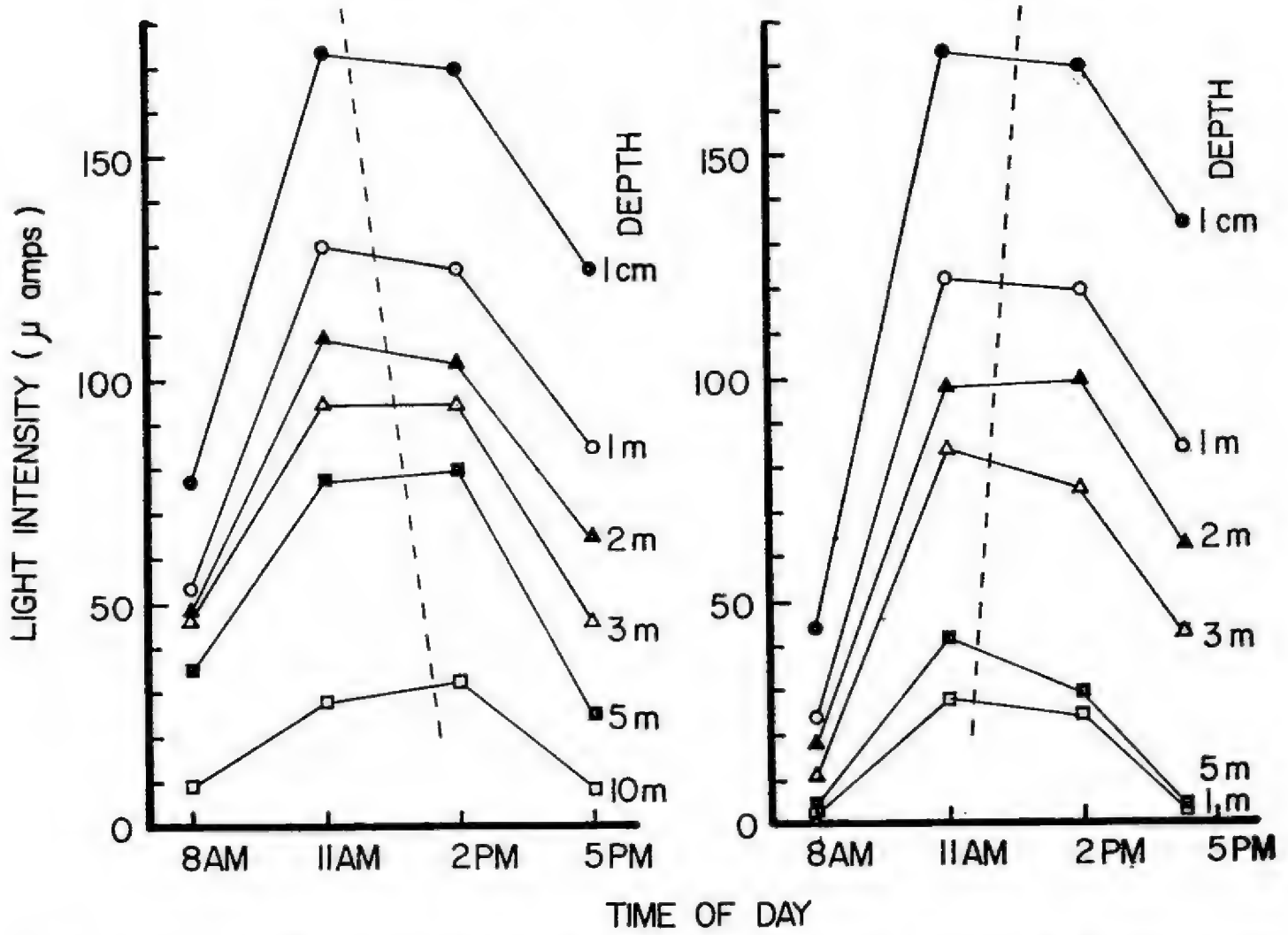

FIG. 3. Light penetration at various depths both inside and outside of the kelp bed at various times of the day. Note the shifts in intensity peaks with increasing depth. The difference found within the kelp bed is attributed to the daytime orientation of the kelp to current and direction of incident light.

Standing Crop of Macrocystis Pyrifera and Undergrowth

Very little data are available on standing crops of *Macrocystis*. Scagel (1947) in his investigation of life history and growth in *M. integrifolia* Bory in British Columbia reports wet weights of one pound per square foot of bottom when the canopy cover is from 30 to 50 per cent (4.88 kg/m^2). Values from 25 to 40 tons per acre (5.64 to 9.00 kg/m^2) were reported for *M. pyrifera* beds at La Jolla, California by Aleem (1956). Other values are derived primarily from harvesting statistics and, therefore, do not include the lower portions of the plants (Tseng, 1947).

To determine kelp standing crop a method utilized by North (1957a) to assess the density of kelp plants per square meter of bottom and a method utilized by Scagel (1947) to assess the average wet weight of plants in a given area were combined. To compare kelp densities, North utilizes a statistic termed the "stipe index"; defined as the number of adult stipes per square meter of bottom. This statistic is obtained by counting the number of adult stipes in a known area (usually along a transect 100 meters long by 4 meters wide) and converting the count to stipes per square meter. In our study several transects 30 meters by 6 meters were used at various depths rather than 100 meters by 4 meters since the length of diving hose restricted longitudinal movement. The distribution of plants along the transect, the number of stipes for each plant, and the bottom substrate configuration were all recorded on underwater board.

In the Paradise Cove beds, average stipe indexes of 4.20, 4.97 and 4.10 were obtained for 6, 9, and 12 meters depth, respectively. North (1957a) reports values of 4.58, 4.59 and 3.45 for the Paradise Cove bed in about 10 to 12 meters depth very close to our study area. The transects for nine meters depth are pictured in Figure 4. The high stipe index obtained at nine meters is considered significant since it represents the center of the Paradise Cove beds. Aleem (1956) has indicated a crowding of individual plants toward the middle of the La Jolla kelp beds, while Thompson (1959) has reported the greatest density to be on the seaward edge of the Santa Barbara kelp beds.

To determine wet standing crop per square meter, individual plants from each depth were removed from the bed, returned to the laboratory, cut into one and one-half meter sections from holdfast to apex, dissected into stipes, bulbs, blades, fruiting blades and holdfast, and each component weighed. In this manner the contribution of each morphologic component of the plant was calculated. In addition, the weight of plant at different depths above the bottom was approximated since the plants were weighed in 1.5 meter sections from the bottom to the top. The average biomass of *Macrocystis* per square meter of bottom was calculated by assuming that the relative proportion of the components of all kelp plants from a given depth were the same. The relative proportion of the components from several kelp plants collected in December, 1958, at Santa Catalina Island, California from similar depths were almost identical with average values obtained for kelp plants from the Paradise Cove beds. The stipe index for each depth was divided by the number of stipes in a mature plant from that depth, and this ratio was multiplied by the total weight of the plant, to obtain the average weight of plant per square meter of bottom. The same ratio was used to calculate the weight of components and sections per square meter.

The average wet biomass of kelp at various depths in the bed, the contribution of each component, and the vertical distribution of biomass of kelp plants at various levels

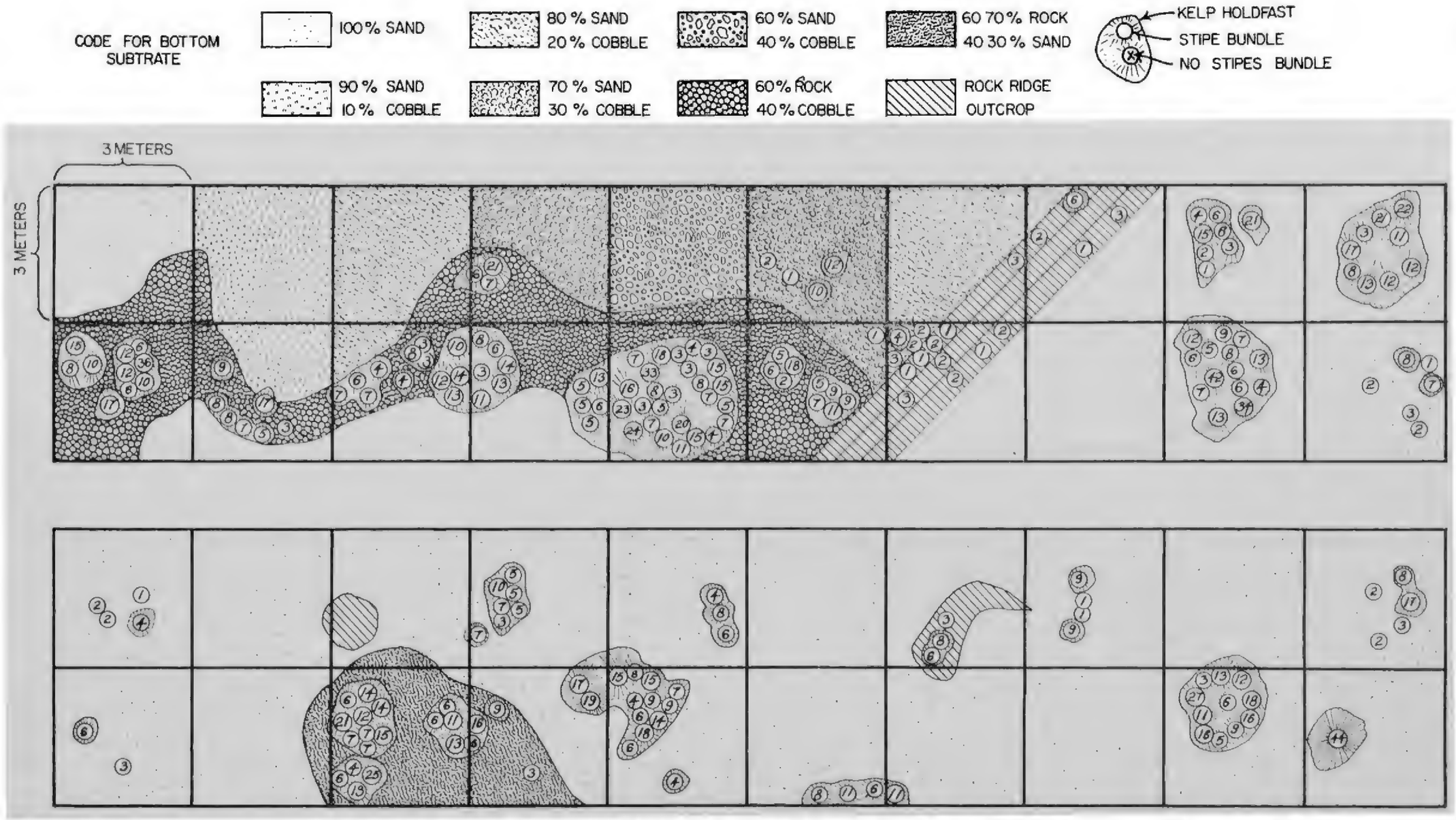

FIG. 4. Bottom quadrats in nine meters depth within the kelp bed. The stipe values of three or less are small kelp plants that did not exceed five to six feet in height. They were not counted in determining the stipe index. Average stipe index for these transects is 4.97. The type of bottom substrate for each three square meter quadrat represents the dominant type as judged by eye.

from the surface to the bottom, are indicated in Figure 5. The high value for nine meters depth in the center of the bed reflects the high stipe index obtained and indicates the denseness of the bed in absolute units.

It is possible to convert the stipe indexes reported by North (1957a) for the Paradise Cove beds to kg/m^2 by the above method. Values of 5.34, 5.34 and 4.00 kg/m^2 are obtained. These conversions are in excellent agreement with values reported here.

From 25 to 43 per cent of the wet kelp biomass is found in the canopy. The actual weight of *Macrocystis* at various levels is subject to considerable variation since both tides and currents cause changes in the amount of plant at the surface. The data presented in Figure 5 are based on the assumption that the plants were oriented straight upward to the surface, a condition that prevails only during very low current velocities (early morning at Paradise Cove). Nevertheless, the values can be considered to approximate the wet biomass at various depths through the kelp bed.

The mean percentage composition of various morphologic components of all plants measured was: holdfast, 14.4%, stipes, 18.5%, bulbs, 14.8%, blades, 50.1% and fruiting blades 2.2%.

The number of blades per square meter for plants from 6, 9, and 12 meters depth were 273, 315, and 275, respectively. These counts reflect the greater density of kelp plants in the center of the bed. The total leaf area index (equals total blade area in m^2/m^2 bottom, Watson, 1956) and the index at various vetrical depths obtained from blade tracings in 6, 9, and 12 meters are presented in Figure 6.

The total index for different depths did not vary greatly, but the vertical distribution indicates that a greater percentage of the total blade area occurs in the crown or surface canopy in six and nine meters depth. A leaf area index of this magnitude is similar to

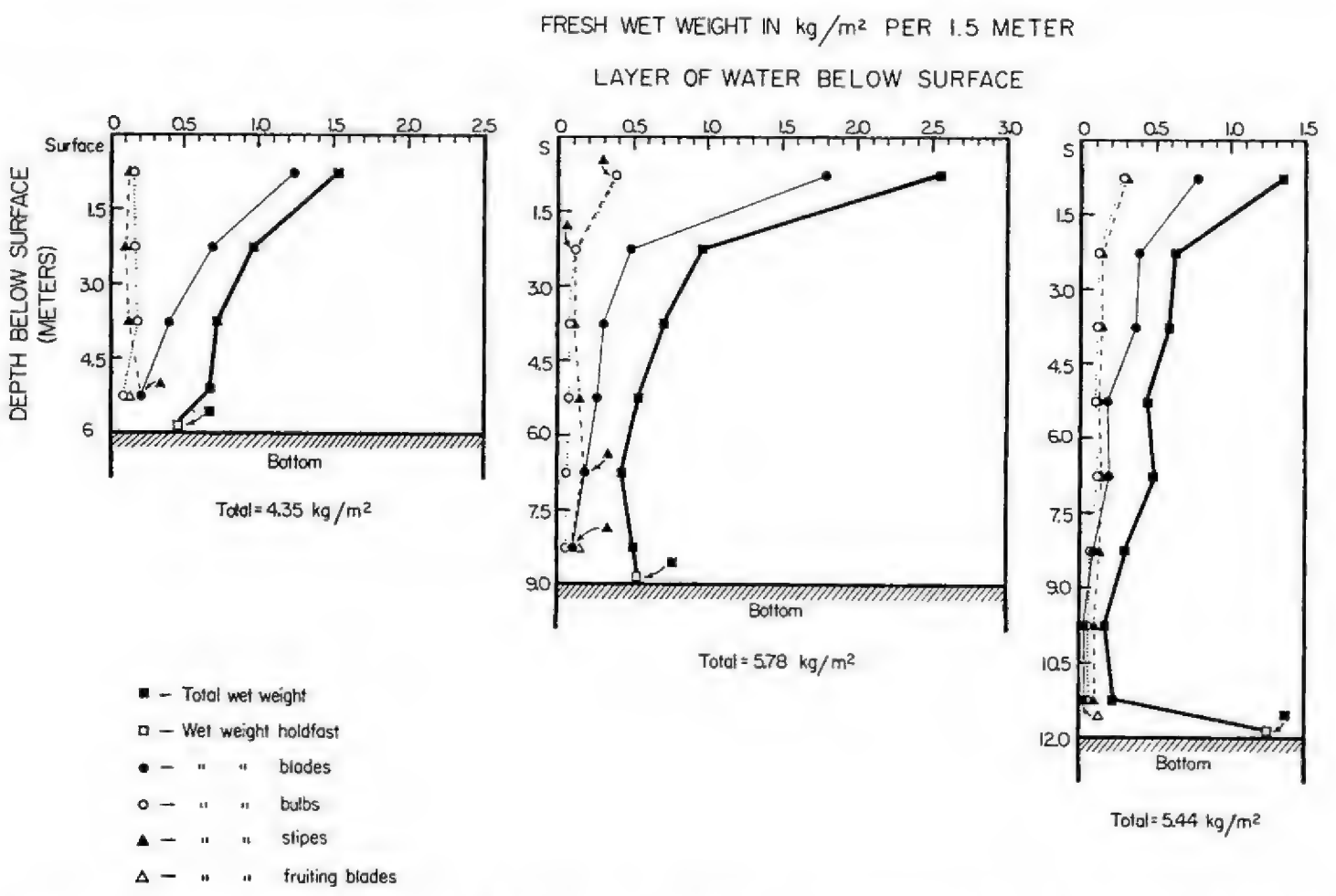
FRESH WET WEIGHT IN kg/m² PER 1.5 METER
LAYER OF WATER BELOW SURFACE
DEPTH BELOW SURFACE (METERS)
Surface
Bottom
Total = 4.35 kg/m²
Total = 5.78 kg/m²
Total = 5.44 kg/m²
■ — Total wet weight
□ — Wet weight holdfast
● — " " blades
○ — " " bulbs
▲ — " " stipes
△ — " " fruiting blades

FIG. 5. Average vertical and total distribution of fresh wet biomass of giant kelp at 6, 9 and 12 meters depth at Paradise Cove. Vertical distribution is presented for the situation when kelp plants are oriented straight upward to the surface, a condition known to exist only during periods of negligible current.

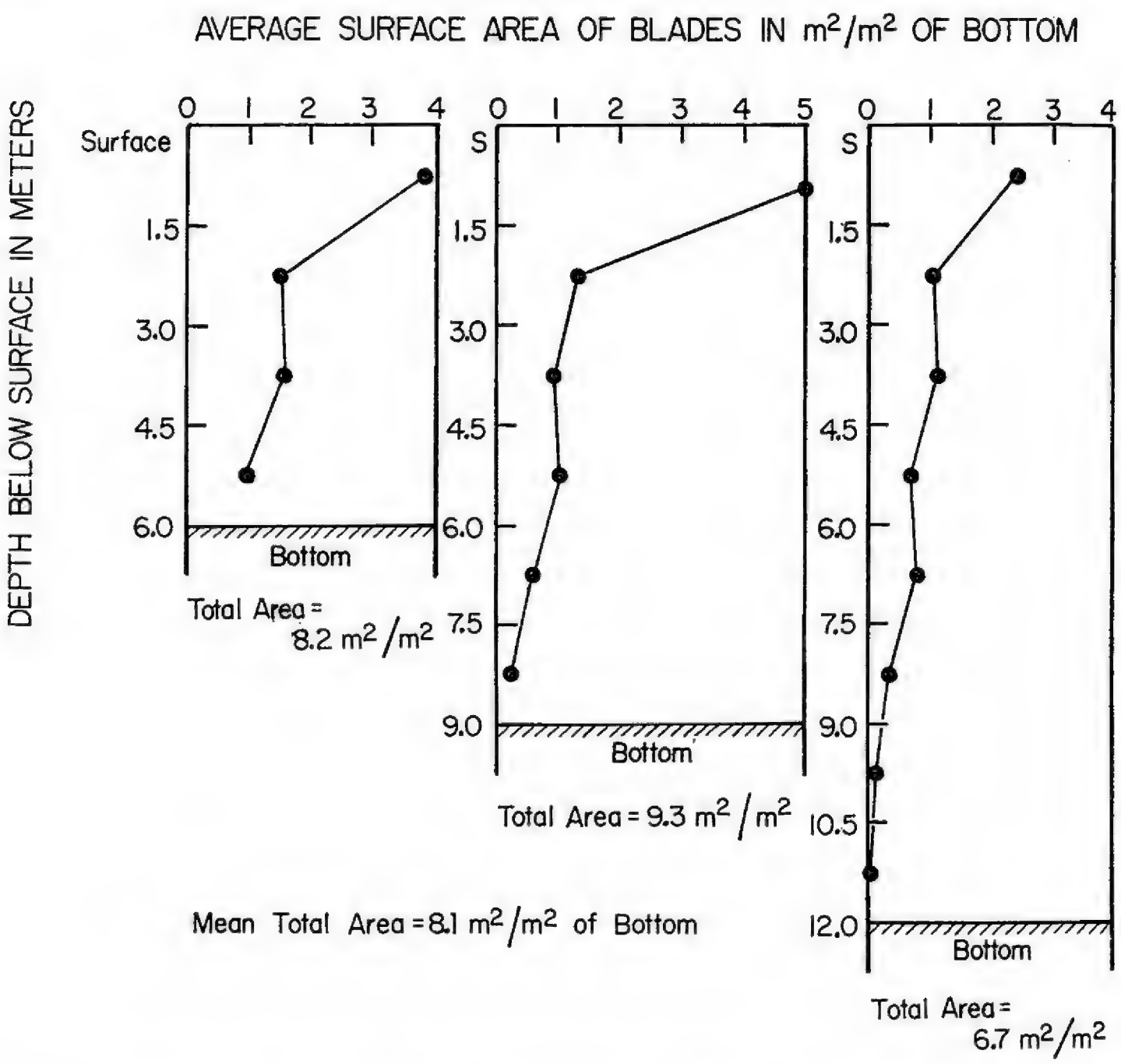
AVERAGE SURFACE AREA OF BLADES IN m²/m² OF BOTTOM
DEPTH BELOW SURFACE IN METERS
Surface
Bottom
Total Area = 8.2 m²/m²
Bottom
Total Area = 9.3 m²/m²
Mean Total Area = 8.1 m²/m² of Bottom
Bottom
Total Area = 6.7 m²/m²

FIG. 6. Average vertical distribution of blade area of kelp blades in square meters/square meter of bottom in 6, 9 and 12 meters depth. Note that the surface canopy (upper 1.5 meters) contains from 35 to 50 per cent of the total blade area.

values for characteristic shade communities (Rainforest, 7, Odum, *et al.*, unpublished; Mangroves, 4, Odum, Golley, and Wilson, unpublished; compared to values of two to three for domestic crops like potatoes, barley, and wheat, Watson, 1956). The high light trapping qualities of kelp canopies and other littoral marine algae (Blinks, 1955) are explained by both high leaf area index and high individual absorption.

Several estimates of the wet standing crop for Laminarine algae have been reported in the literature, particularly for the genus *Laminaria*. Parke (1948) reviews much of this data. For *Laminaria saccharina*, standing crops of 4.7 to 5.7 kg/m² were found along the Murman coast (Kireeva and Schapova, 1933) and from 2 to 8 kg/m² in the Barents Sea (Tikhovskaya, 1940). Walker (1947) found average wet weights of 4 kg/m² for *Laminaria* spp. at the Orkney Islands, while similar values are reported by Gail (1935) for *L. japonica* in the Japanese Sea.

In summarizing a vast amount of distributional data for Scottish laminarines, Walker (1954) reports a decrease in wet weight of plants /m² with depth. Values ranged from 6 kg/m² in one meter depth to 1.2 kg/m² in 10 meters depth with an average of about

3 kg in five meters depth. The regression tends to be exponential and, therefore, is related by Walker to light penetration. Blinks (1955) reports wet weight/m^2 for several genera of littoral marine algae with values ranging from 0.07 to 0.76 kg/m^2 for green and red algae and from 0.75 to 4.4 (*Laminaria*, blades only) kg/m^2 for several brown algae.

Judging from the values found for *Macrocystis pyrifera* and the values reported for other laminarine algae, wet standing crop appears to average between 4 to 6 kg/m^2. In contrast to *Laminaria*, however, *Macrocystis* and probably other algae that form surface canopies maintain rather large standing crops with increasing depth.

Wet Biomass of Undergrowth

Aleem (1956) reports a decrease with increasing depth in wet standing crop of bottom plants under kelp canopies in the La Jolla kelp beds. In seven meters depth he found 2.49 kg/m^2 while in 15 meters, wet standing crop was 1.97 kg/m^2. Such high values for undergrowth were not found in the Paradise Cove beds. Macrophytes in dense stands were observed under the canopy mainly near open areas, such as rock ridges, or below considerable openings in the canopy. The bottom beneath the canopy was mapped using nine square meter quadrats made from pipe and nylon line. A typical quadrat containing high numbers of macrophytes is indicated in Figure 7. This quadrat was placed adjacent to a rock ridge running through the kelp bed. Sub-quadrats, seven and nine of this quadrat, contained relatively dense stands of young *Macrocystis pyrifera, Corallina officinalis, Pterygophora californica*, and *Gymnogongrus platyphyllus*. Wet standing crop was 0.475 and 0.467 kg/m^2 for the macrophytes in sub-quadrats seven and nine. Comparison with the wet standing crop of a square meter quadrat from a rock ridge area which had no kelp canopy indicates close agreement for the macrophytes (0.458 kg/m^2). In contrast, quadrats beneath dense kelp canopies in the center of the bed gave much lower results. In these areas only *C. officinalis* and *G. platyphyllus* were found and only in very small amounts. For nine square meters the average wet standing crop was only 0.004 kg/m^2 (range 0.001 to 0.012 kg/m^2).

On the lithified mud beneath kelp plants several small unidentified algae, less than one-half inch in height, were attached. Estimation of biomass for such forms is most difficult. However, a maximum value was estimated by weighing the plants contained on 1 cm^2 of mud and assuming that each m^2 was entirely mud. Maximum wet standing crop on this basis was 0.044 kg/m^2. Since considerable sand occurred over most of the mud bottom actual standing crops were much less. Encrusting algae (both *Lithothamnion* and *Lithophyllum*) were found on the lithified mud under dense kelp canopies, but they covered only 25 to 30 cm^2/m^2 of bottom. In open areas, where rock substrates were available, the amount of encrusting algae increased considerably, covering 25 to 30 per cent of the rock.

On the basis of these results the minimum wet standing crop of undergrowth probably is not less than 0.02 kg/m^2 while the maximum does not exceed 0.5 kg/m^2. Since a considerable portion of the bottom beneath the Paradise Cove kelp beds lies under dense canopy, the undergrowth on the average probably does not exceed 0.1 kg/m^2. Thus, undergrowth constitutes about two per cent of the total plant biomass within the kelp bed.

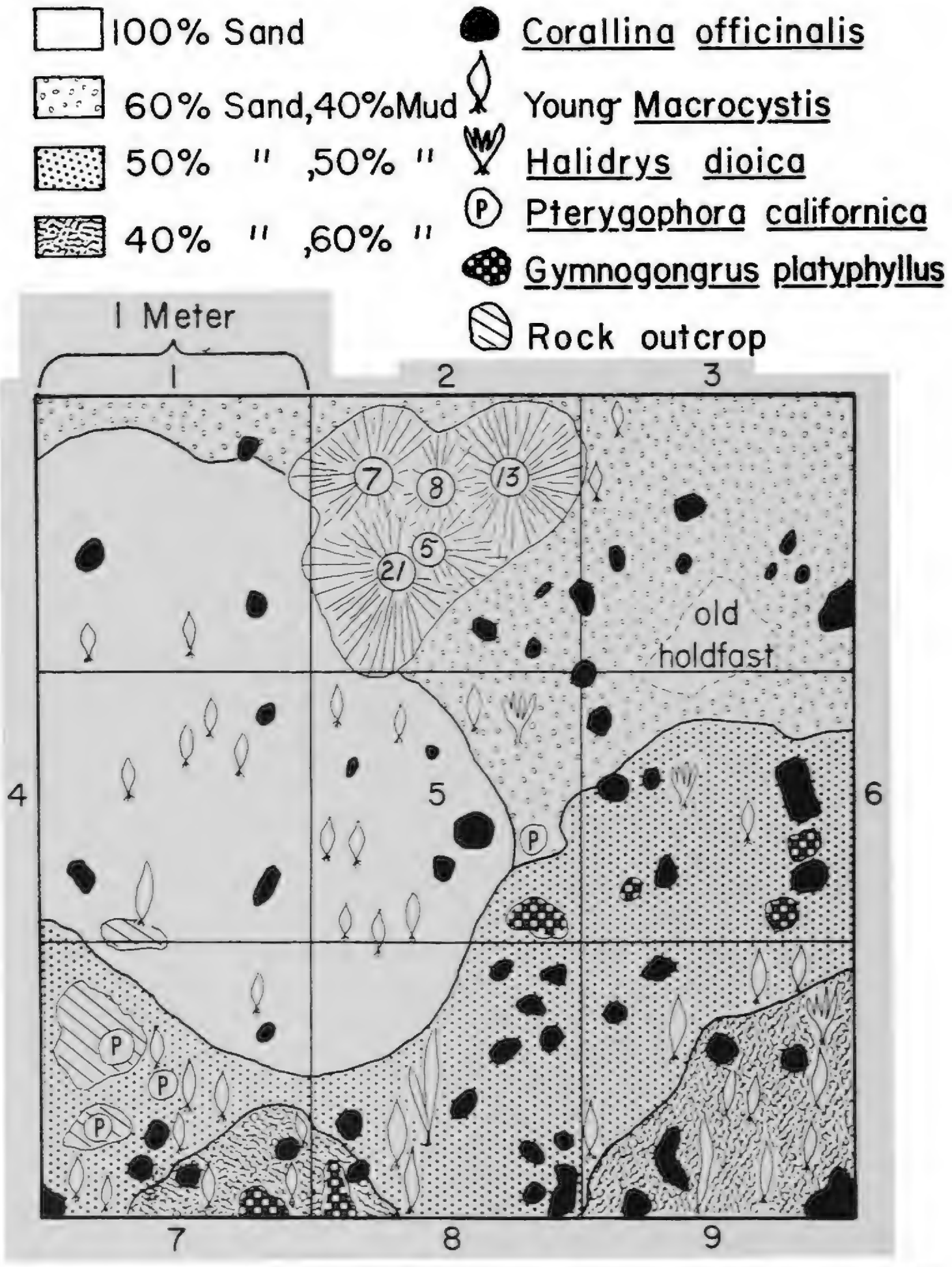

FIG. 7. Typical bottom distribution of algae beneath the kelp canopy in six meters depth. Oher quadrats placed directly under more dense canopies showed a definite decrease in forms such as *Pterygophora* and *Halidrys*. *Corallina* and *Gymnogongrus* still persisted, but in lesser abundance.

Distribution of Chlorophyll "A"

Chlorophyll "A" of the entire community was estimated by extraction of samples of kelp, macrophytic undergrowth, and representative samples of the various types of bottom in 90 per cent acetone after grinding in a mortar and pestle. Chlorophyll (Chl.) was converted into mg/Chl./gm of wet plant tissue or gm/Chl./cm^2 of bottom using a colorimetric method suggested for ecological field analysis by Odum, McConnell, and Abbott (1958).

The chlorophyll content of morphologic parts of *Macrocystis* collected at Paradise Cove are similar to data obtained at Santa Catalina Island (Table 1). Chlorophyll

TABLE 1

Mean chlorophyll "A" content of the various parts of *Macrocystis pyrifera* in mg chlorophyll/gm of wet tissue

	Locality					
	Paradise Cove, June 1959			Santa Catalina, December 1958		
Plant part	Mean chl. mg/gm	Range	No. samples	Mean chl. mg/gm	Range	No. samples
Holdfast	0.026	0.019–0.035	8	0.017	0.008–0.031	5
Stipes	0.043	0.021–0.063	12	0.022	0.014–0.033	6
Bulbs	0.039	0.027–0.054	10	0.012	.....	1
Blades	0.207	0.163–0.278	10	0.218	0.187–0.256	7
Fruiting blades	0.234	0.128–0.310	6	.....	.....	....

content of the blades and fruiting blades was five to six times higher than the content in stipes and bulbs and eight to nine times higher than in the holdfast. Since the amount of each component of the kelp plant per square meter of surface area is known from each depth (Figure 5), the chlorophyll distribution can be readily computed on a weight basis. Results of this calculation are given in Table 2, while the vertical distribu-

TABLE 2

Chlorophyll "A" distribution in various parts of the giant kelp, *Macrocystis pyrifera*

	Chlorophyll 'A' in each component in per cent of total chl./m^2 bottom					
Depth of water in meters	Holdfast	Stipes	Bulbs	Blades	Fruiting blades	Total for entire plant in gm chl./m^2 bottom
6	1.92	4.18	3.86	84.79	5.26	0.62
9	1.81	6.49	3.91	83.13	4.66	0.78
12	5.77	8.50	6.05	77.88	1.80	0.57
Average value	2.99	6.34	4.51	82.15	4.02	0.66

tion of chlorophyll for six and nine meters depth is shown in Figure 10. The results indicate that approximately 80 per cent of the chlorophyll occurs in the blades and that 37 to 58 per cent of this chlorophyll is found in the surface canopy.

Clendenning and Sargent (1957a) have stressed the decentralized nature of photosynthesis in *Macrocystis pyrifera*. They state, "We have found that kelp is remarkably different from land plants of similar size in that it possesses the capacity for photosynthesis in all parts of the sporophyte above the holdfast, as well as at successive stages of its asexual and sexual reproduction. The pear-shaped pneumatocysts and naked cylindrical stipes have about the same photosynthetic capacity per unit of area as the

blades." The distribution of chlorophyll reported here indicates that this is the case, but that only about 12–13 per cent of the total photosynthesis occurs in the stipes and bulbs. Since a large portion of the weight and, therefore, the area of the stipes is displaced toward the bottom (Figure 5) where lower light intensities prevail, it can be expected that their relative photosynthesis is somewhat less than 12 per cent of the total possible.

Chlorophyll content per unit area was also obtained for the blades. A mean value of 36 mg Chl./m^2 of blade (range 31–48) was obtained. A rough approximation of chlorophyll per unit area for the stipes can be calculated since the total length of stipes and chlorophyll content are known for each depth of the kelp bed. Chlorophyll values per square meter of surface area for stipes are 41, 39, 46, and 42 mg/m^2 for 3, 6, 9, and 12 meters. These results are within the range of chlorophyll values obtained for the blades and tentatively suggest that chlorophyll distribution is uniform per unit area in *Macrocystis* blades, stipes, and possibly bulbs.

Chlorophyll "A" of the Undergrowth

Estimates for chlorophyll "A" of macrophytes and smaller bottom attached algae are much less certain than for *Macrocystis*. The heterogeneity of the substrate plus the difficulties in separating functional and non-functional chlorophyll (Odum, McConnell, and Abbott, 1958) in sand, mud, and cobble allow at best only rough estimation.

To check chlorophyll estimates for undergrowth two methods were used in six meters depth. In the first, 12 separate square meter quadrats representing areas with both small and large amounts of macrophytes were mapped and the macrophytes collected, weighed and extracted for chlorophyll. Samples of known area of each type of bottom (sand, mud, rock, etc.) were also extracted for chlorophyll. The chlorophyll content for the twelve square meters of bottom was then averaged. In the second method, a total of three transects (see sample transect, Figure 4) totalling 540 square meters of bottom were mapped and the average chlorophyll per square meter calculated on the basis of extraction of cores and scrapings of known area. Comparison of results gives a mean of 0.18 gm Chl./m^2 (range 0.09–0.50) for the former method and 0.16 gm Chl./m^2 for the latter method. Since the results compare favorably and the latter method was more rapid it was used in nine and twelve meter depths.

Average values for 6, 9, and 12 meters depth are 0.16, 0.14 and 0.12 gm Chl./m^2, respectively. That higher values can be obtained at all depths over dense stands of macrophytes is certain. For instance, in 12 meters depth a stand of *Pterygophora californica*, where this species was most abundant, contained 0.73 gm Chl./m^2, while values of 0.30 to 0.50 were common for macrophytes in open areas in six meters depth.

The total average chlorophyll in grams per square meter of bottom, including kelp and undergrowth, for stations in water 6, 9, and 12 meters deep are: 6 meters, 0.78; 9 meters, 0.92; 12 meters, 0.69; with a mean of 0.74 gm Chl./m^2.

In the preceding section it was pointed out that the undergrowth accounted for about two per cent of the wet biomass on a square meter basis. The undergrowth includes about 20 per cent of the total chlorophyll, because chlorophyll per unit of wet weight of undergrowth is in excess of that in *Macrocystis*. In addition, much non-functional chlorophyll is included in undergrowth since plant fragments are common in bottom samples.

Metabolism of the Kelp Bed

Metabolic measurements of *Macrocystis* have been confined to photosynthetic and respiratory studies of isolated parts of the kelp in the laboratory or in the field (Sargent and Lantrip, 1952; Clendenning and Sargent, 1957a, 1957b, 1958a, 1958b; and Clendenning, 1958, 1959). As yet, however, no information is available on *in situ* metabolism of kelp under natural conditions. If one is to compare productive potentials of kelp communities with other major communities it is necessary to have some index of gross photosynthesis.

Method of Measuring Metabolism in Situ

The diurnal oxygen curve method as used by Sargent and Austin(1949) and later modified to account for diffusion of oxygen from or into the water (Odum and Hoskins, 1958), is at present the most suitable for estimating total community respiration and photosynthesis. This method with slight modification was used to calculate *in situ* metabolism in the Paradise Cove kelp beds.

Diurnal oxygen samples were collected every three hours at one and three meters below the surface in three meters depth and at 1, 3, and 5 meters below the surface in six and nine meters depth. All samples were fixed according to the Alsterberg (Azide) modification of the Winkler method and oxygen concentration determined colorimetrically according to the technique of Beadle (1958). Each sampling station within the kelp bed was marked with an anchored float. It is assumed that water within the kelp bed was not greatly mixed between sampling depths and that the direction of current was parallel to depth contour lines. If these assumptions were valid, absolute increases or decreases in oxygen concentration from successive samplings should represent the rate of community photosynthesis or respiration between sampling periods at each sampling depth. These conditions appear to have been met, except at dawn and dusk during periods of wind shifts (see section on currents).

Gross photosynthesis and community respiration were determined graphically for each station at each depth below the surface. The graphical procedure is shown for the station at nine meters depth, sampled at three meters below the surface, in Figure 8.

Corrections for wind and current shifts. Between periods of wind shifts and consequent changes in current direction at dawn and dusk (due to local land-sea breezes), increases in the oxygen content of the water occurred (Figure 9). This was most evident at dusk when both wind and current velocities were highest. Examination of the oxygen concentration in the water at 1, 3, and 5 meters below the surface (Figure 9), particularly at dusk, shows that increases in oxygen were greater the deeper the sample. The tendency was evident at all stations (Figure 9) and strongly suggests an intrusion of water of higher oxygen concentration into the kelp bed. This intrusion causes a deflection of the diurnal curve upward which, if not corrected in the calculations, will cause overestimation of photosynthesis. Change in temperature was not noted during the intrusion of this water, the temperature remaining constant (18.5° C at surface, 17.5° C at bottom).

To correct for this non-metabolic increase in oxygen content, it was assumed that the changes of rate due to metabolism during intrusion were the same as for the period prior to the intrusion of outside water. The resultant modifications in the rate of change curve are indicated by dashed lines in the upper graph of Figure 8.

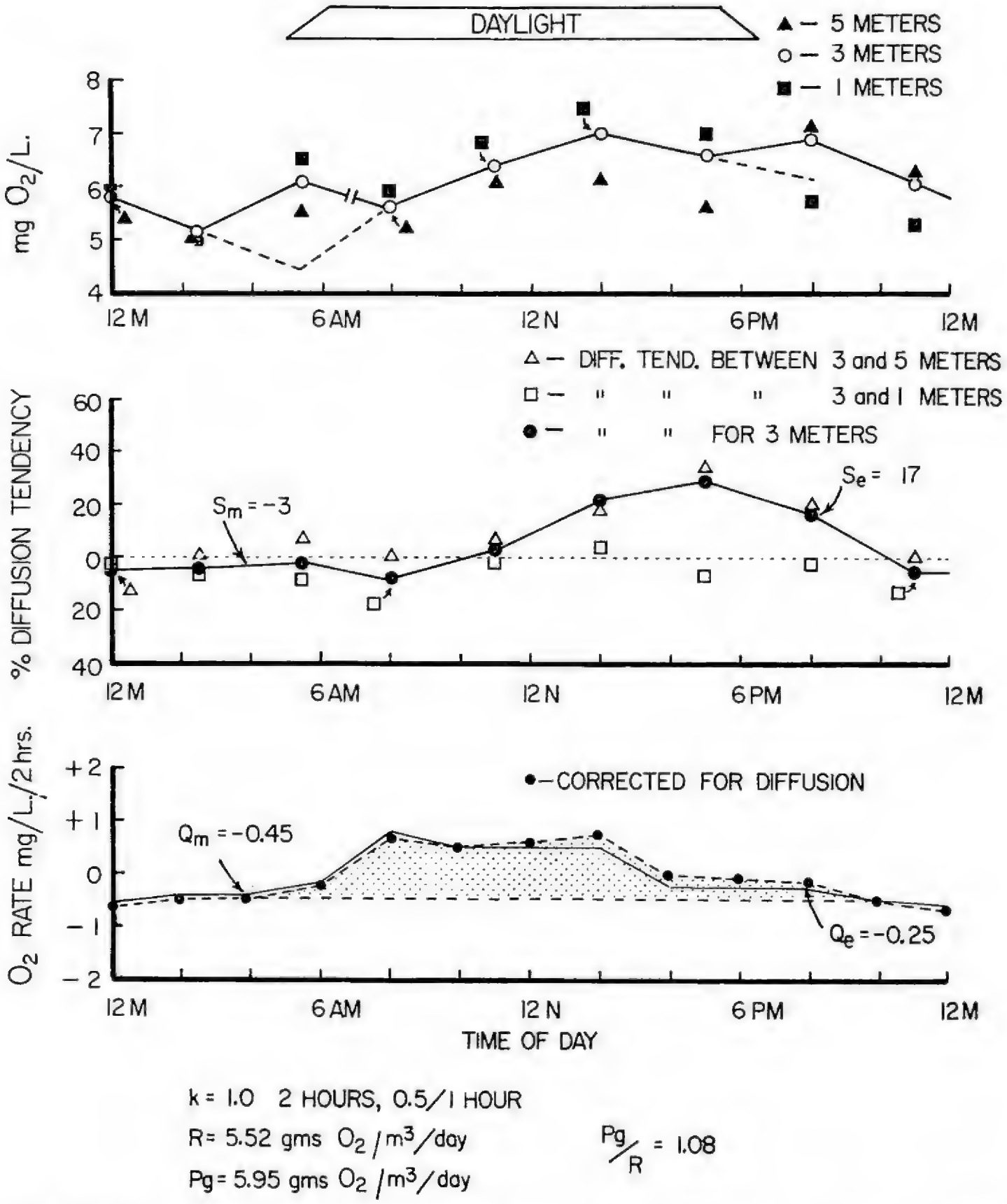

FIG. 8. A typical diurnal oxygen curve obtained at three meters beneath the surface in nine meters depth within the kelp bed. Note the sharp rise in oxygen content due to intrusion of water from below during current shifts before dawn and at dusk especially in deeper water. The dotted lines represent the respiration rate of the community, uncorrected for diffusion, based on the assumption that respiration was constant. The middle graph is the diffusion tendency curve. The lower graph is the diffusion corrected rate of change curve obtained by the method of Odum and Hoskins (1958).

Correction for oxygen diffusion between water layers. In correcting the oxygen rate change curve (solid line, lower graph, Figure 8) for diffusion between air and water it is normal procedure to obtain a diffusion constant, based on the ratio of algebraic difference between the rate change of oxygen and the percentage oxygen saturation of the water before dawn and after dusk. This constant when multiplied times the difference in per cent saturation of the water and 100 per cent saturation relative to air compensates for non-metabolic losses and gains in oxygen due to diffusion. The cor-

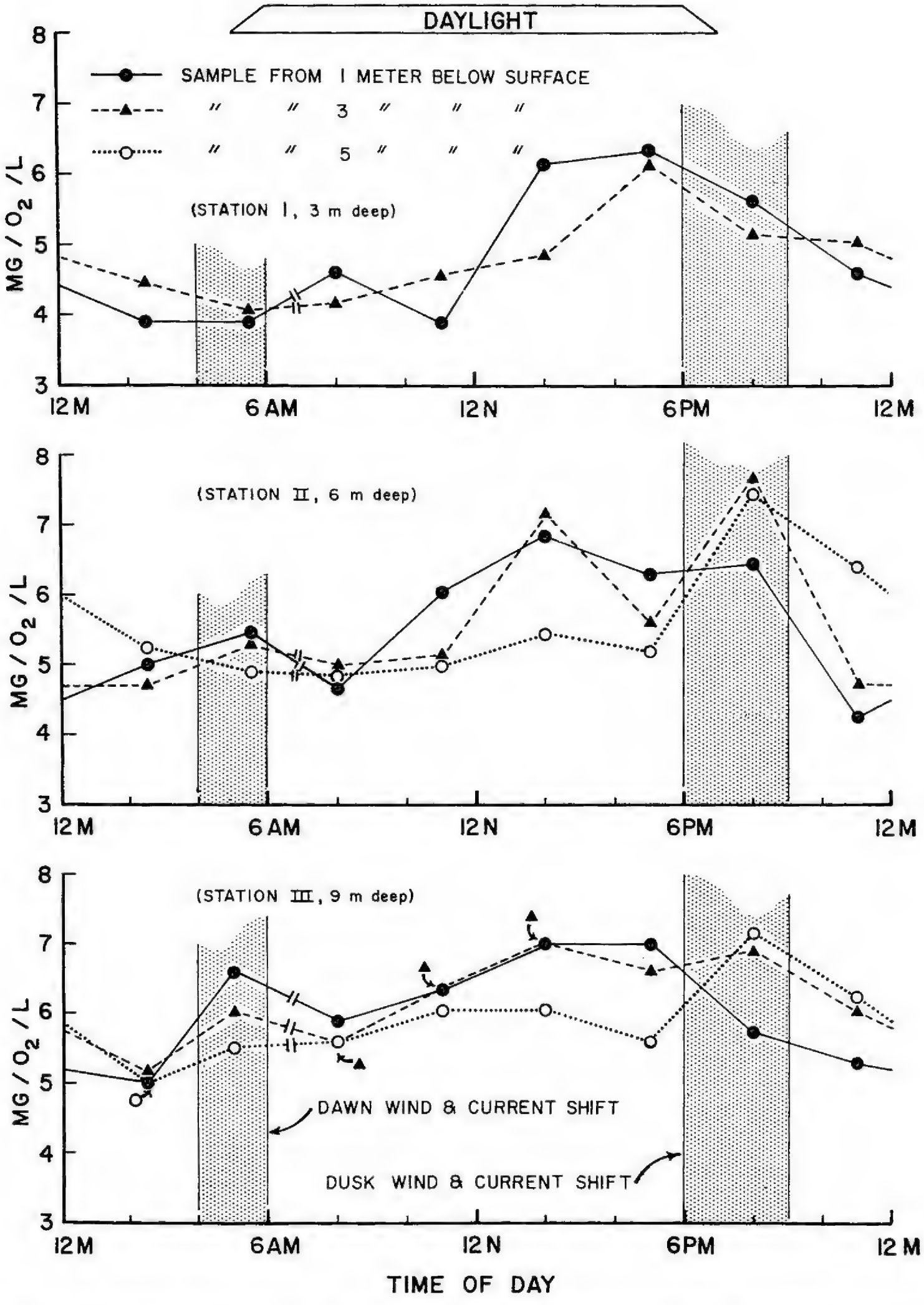

FIG. 9. Diurnal oxygen curves obtained within the kelp bed at Paradise Cove, California. Curves were obtained from samples taken at 1, 3, and 5 meters below the surface at stations I, II, and III (see Figure 1). Data were collected on July 2–3, 1959. Note the sharp increase in oxygen content of the water, particularly for the deeper samples at stations II and III, at dawn and dusk. Increases are correlated with changes in wind direction and current and probably are the result of intrusion of outside water from below.

rection is added or subtracted graphically from the rate change curve depending on whether the water at that time is supersaturated or undersaturated (Odum and Hoskins, 1958). This constant is applicable in rather shallow water communities, but presents difficulties in aquatic communities of more than a few meters depth.

If one considers a layer of water one meter thick at 10 meters depth, and finds that its oxygen concentration is 20 per cent higher than the water layers at 9 and 11 meters depth, it is apparent that oxygen will tend to be diffused upward and downward by eddy mixing. The amount of oxygen that diffuses per unit time will depend on the absolute oxygen differences as well as the temperature, turbulence and other physical properties of the water mass. The tendency for oxygen to diffuse between layers of water below the surface will depend not on its percentage oxygen saturation relative to air, but rather on the oxygen gradient relative to the oxygen content of the water just above and below. For this reason, in analysis of the diurnal oxygen curves obtained at Paradise Cove oxygen diffusion corrections were based on the ratio of the oxygen concentration of the water at a given sampling depth and the oxygen concentration of the water above and below. Each three hour sample at each station was corrected. A specific example should make this clear.

In Figure 8, the middle graph represents the oxygen concentration of the water at three meters depth relative to the oxygen concentration at one and five meters depth through 24 hours. To obtain this line, the oxygen concentration at a given time was divided by the oxygen concentration at one meter and at five meters depth (black triangles and black squares). These ratios are called "diffusion tendency." The total "diffusion tendency" was obtained for the 24 hours by plotting the algebraic sum of these percentage ratios. It can be seen that from about 11 AM to about 10 PM there was a marked tendency for oxygen to diffuse outward from the layer at three meters depth, while during the rest of the day there was a slight tendency for oxygen to diffuse in. In essence, this means that photosynthesis will be considerably underestimated and respiration slightly underestimated if not corrected for diffusion. The use of the curve of "diffusion tendency" is completely homologous in principle with the use of the percentage oxygen saturation curve for the graphical method suggested by Odum and Hoskins (1958). In fact, once the "diffusion tendency" curve is plotted the diffusion constants and consequent corrections are applied in the same manner.

Metabolism

Gross photosynthesis (P_g) and respiration (R) in grams oxygen/m^3/ 24 hours are shown graphically for various depths (Figure 10). Vertical distribution of fresh wet biomass and chlorophyll for each depth per square meter of surface area are also graphed in Figure 10. Respiration just beneath the surface was high. Interestingly, respiration was also high in three meters depth beneath the surface canopy in six and nine meters depth. The trend of community respiration with depth was similar at all three stations sampled, and with but slight deviation, parallels the decrease in the vertical distribution of wet biomass. In contrast, P_g does not decline with decreasing biomass and chlorophyll content, but rather increases sharply at three meters below the surface (Figure 10). As might be expected, at five meters below the surface where light intensities are less, gross photosynthesis falls off.

The lower P_g obtained for the surface water seems paradoxical since both the wet weight of kelp and the chlorophyll content are largest in the upper 1.5 meter of water

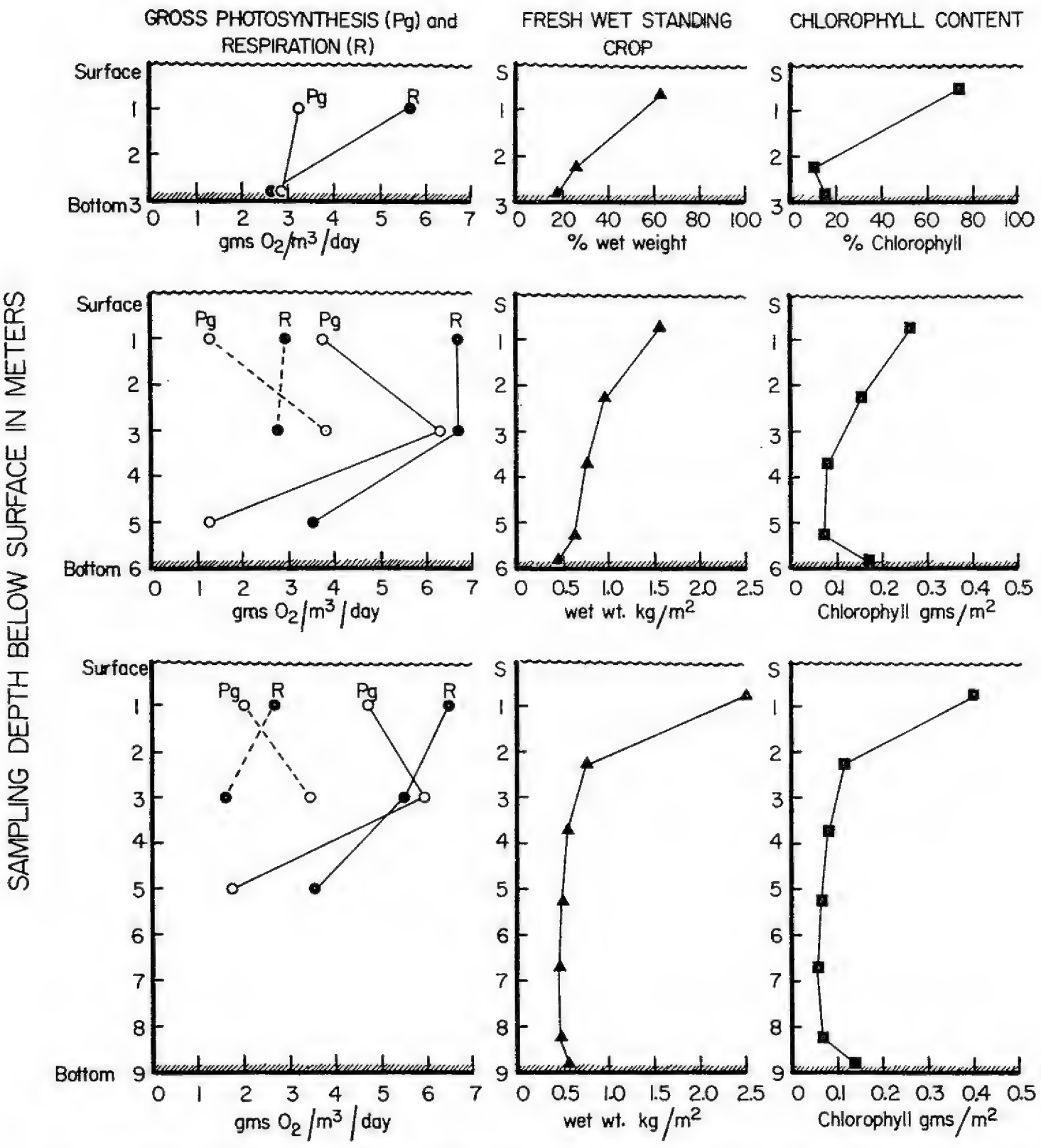

FIG. 10. Gross photosynthesis (P_g), respiration (R), vertical distribution of wet biomass and vertical distribution of chlorophyll 'A' for the Paradise Cove kelp bed in 3, 6 and 9 meters depth. The dark lines for the P_g and R graphs represent the total metabolism including plankton. The dotted lines represent the total P_g and R for the kelp community minus the planktonic P_g and R. The values for P_g and to a lesser extent R for the surface water are underestimated.

(Figure 10). Clendenning and Sargent (1957b) have demonstrated that summer surface blades show lower photosynthetic capacities than blades from intermediate depths, but even in summer photosynthesis was in excess of respiration. Photosynthesis did not balance respiration in sickly blades, a condition that was not found in the Paradise Cove beds. In their study of the La Jolla kelp beds, Sargent and Lantrip (1952) using light and dark bottle methods found that photosynthesis of summer surface blades exceeded respiration at surface temperatures similar to the temperatures reported here. Similar results were obtained, when using bottle methods, by Clendenning for several southern California kelp beds (personal communication).

It seems likely, therefore, that values for P_g and probably also for R of the upper meter

of water are underestimated. Whether underestimation actually occurred and if so what caused it is unknown, but the interaction of swell, changing current direction and velocity, and a possible scouring action of the kelp canopy that might enhance gas exchange with the atmosphere are suspect.[4] In fact, the surface canopy blades often are in direct contact with the atmosphere when they float at the surface. Whether the total blade exposure is sufficient to effect a large gas exchange is difficult to assess.

Two types of data indicate that the surface P_g and R values are underestimated. First, the mid-day peaks in oxygen for the surface water do not exceed peaks from three meters below the surface (Figure 9) and indicate that a high gas diffusion to the atmosphere may have occurred. Second, the results of diurnal pH curves (see section on pH) show that surface water was more acid than layers at three or five meters depth. Since changes in pH primarily reflect CO_2 released or absorbed by the biotic community and, also, since the high buffering action of sea water would restrict CO_2 exchange with the atmosphere it seems probable that the surface metabolism of the kelp community based on oxygen criteria was underestimated. Because of the uncertainties involved no corrections have been made in Figure 9 to increase the values of P_g and R at the surface for the various stations.

Phosphorescence within and without the kelp bed during the night indicated the presence of plankton in the area. A diurnal oxygen series was obtained outside the kelp bed for one meter and three meters below the surface in approximately 20 meters depth. Total respiration and gross photosynthesis in gm O_2/m^3/day were: one meter, $R=3.8$, $P_g=2.5$; three meters, $R=3.9$; $P_g=2.5$. The results indicate homogeneity in the upper four meters. Respiration was far in excess of photosynthesis.

If it is assumed that the upper four meters of water within the kelp bed contained the same planktonic community it is possible to estimate the respiration and gross photosynthesis of the kelp community by subtracting out the planktonic R and P_g. The dotted lines in Figure 10 indicate the adjusted respiration and gross photosynthesis for the kelp community minus the plankton for six and nine meter depths.

At three meters depth gross photosynthesis of kelp was in excess of respiration (mean P_g/R six and nine meters $= 1.8$). A similar ratio probably would have been obtained for the surface canopy, but it cannot be calculated because of the low and underestimated P_g obtained for the upper meter of water.

It is interesting to compare the data reported by Sargent and Lantrip (1952) for respiration in *Macrocystis* (0.41 ml O_2/gm dry weight/hr.) with the respiration obtained in this study. Converting their data, a respiration of 2.9 mg O_2/gm wet weight/day is obtained. Multiplying this value times the fresh wet weight of *Macrocystis* in the upper 4.5 meters for six and nine meters depth (Figure 5) and correcting to 4 m^3, values of 8.9 and 9.8 gm $O_2/4\ m^3$/day are obtained, respectively. Doubling and summing the values in Figure 10 at one and three meters below the surface for six and nine meters depth gives 11.4 and 8.8 gm $O_2/4\ m^3$/day, values that agree with Sargent and Lantrip's results.

John Prescott examined the Paradise Cove beds in August approximately one month

[4] The action of swell causes a constant change in velocity of surface water particles in a vertical and to a lesser extent a horizontal direction. Such changes would cause not only a constant mixing, but also changes in pressure which would affect the oxygen saturation properties of the water. Since oxygen saturation values are based on static water, the per cent saturation values utilized in calculation of diffusion corrections in the diurnal oxygen curve method would necessarily be low. Such low values would result in underestimation of gross photosynthesis and respiration, a tendency in keeping with the conflicting data reported here for the upper meter of water.

after the conclusion of this study. Temperature of the surface water had risen to 22.5°C, but was still only 18°C near the bottom. Approximately 80 to 90 per cent of the heavy surface canopy which was present in early July had disappeared. Since P_g/R was not far removed from unity it is possible that the increases in temperature which occurred could have resulted in a sufficient increase in R to upset the photosynthetic balance of the community and result in canopy disappearance.

Diurnal pH Changes

Changes in pH were measured concurrently with oxygen throughout 24 hours at 1, 3, and 5 meters below the surface in 3, 6, and 9 meters depth (Stations I, II, and III, Figure 1). A Beckman portable pH Meter (model N) was used. The diurnal pH curves for nine meters depth are indicated in Figure 11. An increase in pH with increase in depth is apparent throughout the day. Similar curves were obtained in three and six meters depth. The constantly lower pH at one meter beneath the surface and to a lesser extent at three meters are probably the result of the higher community respiration found in the surface and sub-surface kelp canopy (Figure 10). A rise of pH during the morning hours and a decrease during the afternoon at all sampling depths and at all stations correlates with the rise and decrease of oxygen resulting from photosynthesis. In contrast to the oxygen data, daytime pH changes indicate that photosynthesis was higher in the surface water than at three meters depth since greater amounts of CO_2 are needed to produce equal changes in pH the lower the pH. Increases at dawn and dusk, similar to the increases found for oxygen (Figure 9), occur but are not as consistent for all samples.

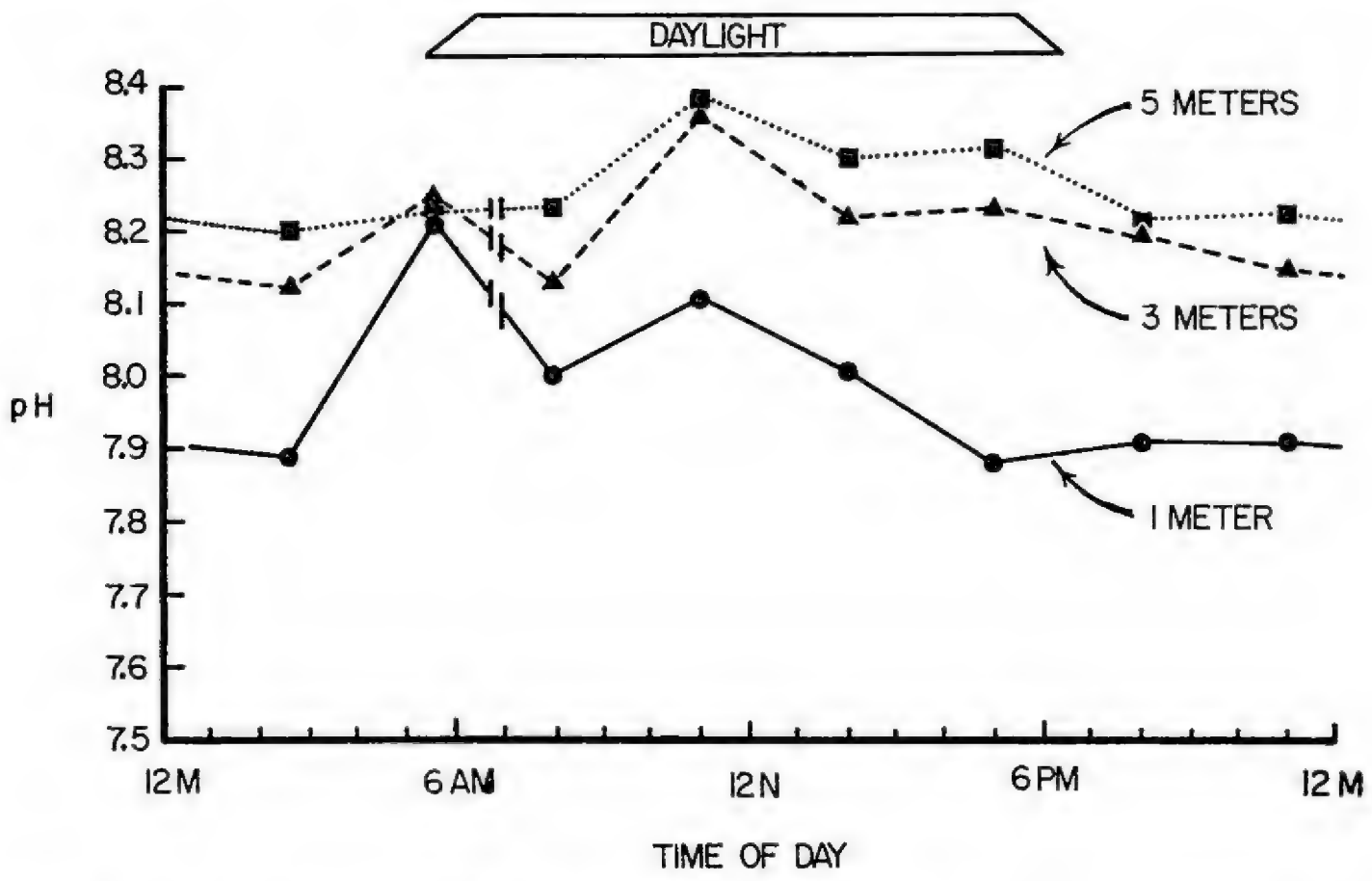

FIG. 11. Diurnal changes in pH obtained from samples collected at nine meters depth within the kelp bed. Note that the pH increases with depth at any sampling time. The lower pH's obtained at the surface are believed to represent the higher respiration of the surface canopy. Diurnal pH curves for three and six meters depth within the kelp bed showed the same differences.

Assimilation Number and Comparison of the Giant Kelp Community with Other Major Ecosystems

Assimilation numbers (gm O_2/gm Chl./hr.) for the Paradise Cove kelp community at six and nine meters depth (Stations II and III, Figure 1) are in agreement (Table 3). However, since the values are based on total community gross photosynthesis which includes the planktonic photosynthesis and since the chlorophyll content for the plankton is unknown, the results are probably at least 10–20 per cent too high. The actual assimilation number for July and August was probably closer to 1.0 (Table 3).

TABLE 3

Assimilation numbers for the kelp community

Relation to depth	6 meters depth	9 meters depth
Entire water column	1.21*	1.26*
2 to 4 meters below surface	2.10	2.18

* Value does not include chlorophyll content of plankton. Actual value is probably nearer to 1.0 (based on average of chlorophyll of plankton obtained from Odum, McConnell and Abbott, 1958).

Assimilation numbers for two to four meters below the surface in six and nine meters depth are given in Table 3. The values are calculated on the basis of chlorophyll content of kelp/m^3 and gross photosynthesis minus the plankton gross photosynthesis/m^3.

A tabulation of assimilation numbers and of chlorophyll "A" in gm/m^2 for a variety of communities are presented by Odum, McConnell, and Abbott (1958). The kelp community at Paradise Cove, with an average chlorophyll content of 0.74 gm/m^2 (range, 0.69–0.92), has a similar chlorophyll content per square meter to a variety of other communities, such as, a coral reef (0.5 gm/m^2), intertidal seaweeds (0.5–1.5 gm/m^2), a variety of euryhaline grass flats (0.43–1.0 gm/m^2), blue green algal mats (0.28–0.66 gm/m^2), some mountain streams (0.3–1.6 gm/m^2), and a variety of terrestrial associations like beech forest (1.3 gm/m^2), birch forest (0.9 gm/m^2), and live oak (0.51–1.68 gm/m^2). The assimilation number for the Paradise Cove kelp community fits the range of values given for most of these communities. Both wet standing crop (4.35 to 5.78 kg/m^2) and respiration (estimate 33–37 gm O_2/m^2/day including plankton; from 13–15 gm O_2/m^2/day excluding plankton) are high. This suggests a community with high production (Odum and Odum, 1955, p. 314). Actually, the gross photosynthesis was also high (estimate 31–36 gm O_2/m^2/day including plankton; from 13–16 gm O_2/day minus plankton; estimates assume surface P_g was equal to or slightly higher than P_g at three meters depth) and directly reveals a high production. The growth rates of two to three inches per day reported by Scagel (1947) for stipe elongation in *Macrocystis integrifolia*, as well as the high photosynthesis to respiration ratios reported in laboratory studies of *M. pyrifera* for various parts of the kelp (from 4.1–22.0) by Clendenning and Sargent (1957b), would indicate a high productive capacity.

As an ecologic unit, the giant kelp community as here represented by *Macrocystis pyrifera* at Paradise Cove, at least tentatively must be considered to have a productive capacity of the same magnitude as other highly productive natural ecosystems. Further study of the intricate trophic relationships and energy flow into, within, and out of the kelp community may eventually permit the balancing of an energy budget and provide for more exacting comparisons with other ecosystems.

Summary

1. Wet standing crop, chlorophyll content, and *in situ* metabolism of a giant kelp community, *Macrocystis pyrifera*, were studied at Paradise Cove, California.

2. Wet standing crop varied from 4.35 to 5.78 kg/m^2. Standing crop of kelp undergrowth amounted to an average of two per cent of the kelp standing crop. Approximately 50 per cent of the wet standing crop was found to occur between the surface and 1.5 meters below the surface.

3. Chlorophyll content varied from 0.69 to 0.92 gm/m^2. Approximately 80 per cent of the chlorophyll in the kelp was found in the blades whereas approximately 50 per cent of the chlorophyll was concentrated in the upper 1.5 meters of water.

4. Gross photosynthesis (P_g) and respiration (R) were measured at various depths within the kelp bed with the diurnal oxygen method. Total community R varied from 33 to 37 gm O_2/m^2/day while P_g varied from about 31–36 gm O_2/m^2/day.

5. Assimilation numbers (gm O_2/gm Chlorophyll/hour) were approximately 1.0 for the entire community. In the sub-surface canopy assimilation numbers were 2.1 and 2.2 for the kelp community minus the plankton.

6. The kelp community is compared to other natural ecosystems. It is concluded that the kelp community has a productive capacity similar in magnitude to that of a coral reef, some springs, and marine grass flats. The shading capacity of the kelp community is found to be of the same magnitude as a tropical rain forest.

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Diurnal Inorganic Phosphate Variations in Texas Bays[1]

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Introduction

Observations by Newcombe and Brust (1940) and Pratt (1950) on the diurnal cycle of inorganic phosphate suggested that daily variations might be observed in the bays of South Texas. Preliminary work reported by Hood (1953) indicated that the inorganic phosphate content of Corpus Christi Bay and the Northern Laguna Madre ranged between 0 and 0.35 microgram Atoms/1. Since the area in question is known to be highly productive (Odum and Hoskins, 1958; Park, Hood, and Odum, 1958), it appears that a rapid turnover of phosphate is necessary in order to maintain the high rates of growth observed.

According to the usual concepts, the inorganic phosphorus of the water is taken in by phytoplankton and fixed into organic phosphorus during photosynthesis. The phosphorus is then regenerated to the inorganic form during metabolism of bacteria, phytoplankton, zooplankton, and higher organisms of the water medium. Uptake would be expected to occur largely in the light, but Harvey (1955) indicates that *Nitzchia closterium* takes up phosphorus in the dark if the cells are growing in low prosphorus medium. In fertilized salt water ponds, Pratt (1950) showed that regeneration of inorganic phosphates from dissolved organic phosphorus depends on the phytoplankton standing crop and shows little realation to the change in population size. The rate of phosphorus uptake is significantly correlated with the size of the phytoplankton standing crop but shows an even stronger dependence upon phytoplankton growth.

An active exchange between dissolved phosphorus and phosphorus present in solid material in the water and mud has been observed by Coffin *et al.* (1949), Hayes and Phillips (1958), and Hutchinson and Bowen (1957).

It appears that either rapid cycling of the inorganic phosphorus or a dynamic exchange with bottom muds and suspended material is functional in providing sufficient phosphorus for the productivity observed in the South Texas bays. This study was undertaken to obtain experimental evidence of phosphate turnover in Texas Bays.

HYDROGRAPHY

The area under study is a part of the Aransas Hydrographic System which includes a number of bays extending from Espiritu Santo Bay to the Laguna Madre. The bays

[1] Contribution from the Department of Oceanography and Meteorology of the Agricultural and Mechanical College of Texas, Oceanography and Meteorology Series No. 161 and The University of Texas; based in part on investigations conducted for the Texas A & M Research Foundation through National Science Foundation Grant NSF-G5038, the Dow Fellowship in Chemical Oceanography, and a summer stipend from the Institute of Marine Science in 1957.

are separated from the Gulf of Mexico by a series of barrier islands whose Gulf Beach forms a broad arch extending in a northeasterly, southeasterly direction. The inner shores of these islands are extremely irregular, indented by ponds and short bayous. The width of the barrier islands varies from somewhat less than a mile in several places to about 4½ miles near the northern end of St. Joseph Island. Other bays, which lie immediately behind these islands are the segmented fragments of the Coastal Lagoon. They vary from five to six miles in width between the inner shores of barrier islands of the mainland shore, except for San Antonio and Corpus Christi Bays, which are embayed river mouths cutting through the mainland shore. Behind these components of the Coastal Lagoon is a series of back bays, which are rejuvenations of a former coastal lagoon. These include Nueces, Copano, and Alazan Bays.

All the bays involved are comparatively shallow; the deepest, Corpus Christi Bay, has a maximum depth of 15.5 feet, followed by Aransas Bay with a maximum depth of 14 feet. The average depths in the stations selected for this study did not exceed six feet in depth. The proportions of these bays are given by Collier and Hedgpeth (1950), and a map of the region including the station locations for this study is given by Park, Hood, and Odum (1958).

The long-term monthly weather averages for Corpus Christi, Texas, which lies in the center of the bay system, is given in Table 1. It will be noted that there is a rather even distribution of rainfall with a maximum occurring in September. The total average rainfall is 26.4 inches per year. Predominate wind in this region is southeast at an average speed of nearly 12 knots.

The exchange of water between the Gulf of Mexico and the bays occurs entirely through Aransas Pass. Interlocking waterways, including a barge canal extending to Brownsville, Texas, are the only means of water transport. The circulation is largely wind driven, although some tidal effect is observed. The flushing rate of Corpus Christi Bay with the Gulf of Mexico has been found to be quite slow (Hood, 1953). Since Baffin Bay must exchange with the Laguna Madre and it with Corpus Christi Bay before exchanging with the open gulf, it is likely that the gulf water contributes little to the biology and chemistry of Baffin Bay and Laguna Madre except on a very long term basis or during periods of unusual flushing.

Methods

1. *Inorganic Phosphorus.* The method used in this study is that of Proctor and Hood (1954) which is based on the observation of Denigis (1920) that the phosphomolybdate complex is soluble in organic solvents and may be reduced in the organic phase with the development of a blue color.

TABLE 1

Long term monthly averages of weather data at Corpus Christi, Texas

	Years of record	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Rainfall in inches	60	1.56	1.48	1.60	1.78	3.22	2.59	1.53	2.27	4.49	2.47	1.99	1.45
Air temperature in °F	60	53.6	56.8	63.0	68.9	74.6	79.3	81.8	81.8	78.6	70.8	62.8	56.6
Relative humidity in %	43	79.0	78.0	71.3	77.6	78.0	77.3	76.3	74.3	76.3	75.9	76.3	77.0
Average wind velocity in knots	62	10.8	11.8	13.4	14.3	14.0	13.1	12.2	11.6	10.8	10.3	10.6	10.4

Phosphomolybdenum blue is thus concentrated, the salt effect is reduced, the color stability is greatly increased, and greater sensitivity becomes practical with standard colorimetric equipment. Interference from citrate, silicate, arsenate, nitrate, fluoride, oxalate (Berenblum and Chain, 1938) and other unspecified ions (Rodden, 1950) are also reduced or eliminated.

Samples, 75 ml in size, were transferred to 200 ml separatory funnels. Five ml of 18 N H_2SO_4 and 5 ml of 10 per cent ammonium molybdate were added to each sample. The samples were swirled in the funnel while adding these reagents so that local concentrations did not build up. After addition of 15 ml of isobutyl alcohol to each funnel, the funnel was shaken for one minute to extract the phosphomolybdate complex. The water layer was discarded. The organic layer was back-extracted once with 25 ml of 1.2 N H_2SO_4. Ten ml of 2 per cent $SnCl_2$ in 2.4 N HCl was added, and the funnel was shaken for one minute. The water layer was discarded, and 5 ml of the isobutyl layer were mixed with 0.5 ml of isopropyl alcohol. Absorbency was read at 730 millimicrons in a 1.2 cm test tube. In the field, the Klett-Summerson photocolorimeter was used to determine absorbency.

2. *Organic Phosphorus.* In this study, total phosphorus was determined in the same way as the inorganic phosphorus after digestion by the method of Hansen and Robinson (1953). This method involves the use of perchloric acid digestion which has the following advantages over other oxidative methods: the interfering impurities present in perchloric acid are of small magnitude; the organic matter is quickly oxidized by the perchloric acid; and the salts formed during digestion are very soluble in water.

3. *Particulate Phosphorus.* The phosphorus which is included in the analysis of particulate matter depends upon the method of separation and washing of the material. In this study the samples were filtered through millipore filters (0.45 micron pore size) thus retaining the particulate organic phosphorus of the phytoplankton, zooplankton, bacteria, and detritus. The material was washed with one 10 ml portion of distilled water while being stirred with a rubber policeman. The water was then drawn through the millipore filter and the material was transferred to a 250 ml Erlenmeyer flask by washing and the aid of a camel's hair brush. Digestion was accomplished in the manner described for total phosphorus. The volume was made up to 50 ml with the addition of phosphate-free artificial sea water and phosphorus was then determined colorimetrically by the method used for inorganic phosphorus.

Diurnal Study in the Field

The results obtained from analysis for inorganic phosphate, total phosphorus, and particulate phosphorus in Baffin Bay on July 26 and 27, 1957, are shown in Figure 1. Data obtained simultaneously for variation in oxygen and in pH are shown in Figure 2 with methods used earlier (Park *et al.*, 1958). Similar data were obtained at the same station in Baffin Bay on August 15 and 16 under conditions of somewhat higher wind stress. These data are shown in Figures 3 and 4. Data from the Laguna Madre Station obtained on August 1 and 2, 1957, are shown in Figure 5 with the parallel oxygen and pH data presented in Figure 6. Data for Redfish Bay are given in Figures 7 and 8.

These results indicate a characteristic increase of inorganic phosphate following the hour of sunset and a corresponding decrease beginning with early morning sunrise. Although considerable variation seems to exist in the different environments, even within

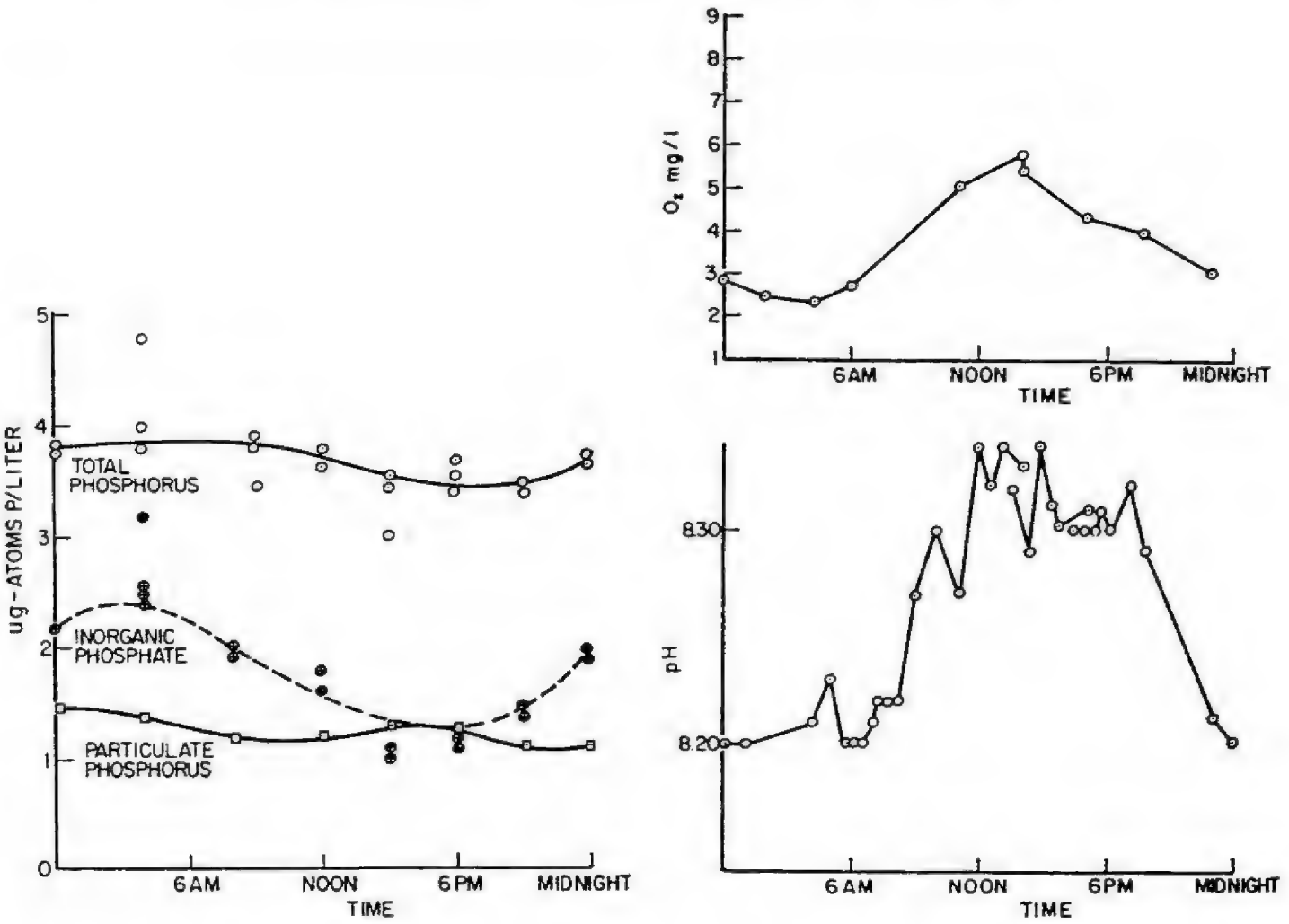


FIG. 1. Diurnal variations in inorganic phosphate, total phosphorus, and particulate phosphorus in Baffin Bay, July 26–27, 1957. Sky, clear; Wind, 10–12 mph; Salinity, 57.4 ppt.

Fig. 2. Diurnal variations in oxygen and pH. Baffin Bay, July 26–27, 1957.

short-time intervals, there is general agreement with respect to the occurrence of higher concentration of inorganic phosphate during the hours of darkness. These results are similar to those obtained by Newcombe and Lange (1939) and Newcombe and Brust (1940) in their studies of the estuarine water of Chesapeake Bay near Solomon Islands, Maryland, except that much less diurnal effect was observed.

A comparison of the diurnal oxygen, pH, and phosphorus of the Texas environments definitely indicates the relationship between inorganic phosphate variations and the amount of photosynthetic activity. Gardiner (1937) has presented evidence which indicates that organisms can liberate phosphates in sufficient quantities to account for at least part of the observed fluctuations. Harvey (1940) has shown that sodium nucleinate and caseinate when added to sea water are rapidly broken down by bacterial action, and the phosphate produced was then utilized by phytoplankton in the cultures. The evidence suggests that planktonic organisms excrete considerable amounts of readily hydrolyzable, low molecular weight, organic phosphate deriviatives, or perhaps even inorganic phosphate.

In our studies, the total phosphorus concentration remains fairly constant as does the particulate phosphorus. The greatest variation in these two fractions occurred in Baffin Bay, on August 15th and 16th. The total phosphorus as well as the particulate phosphorus increased from about 1200 CST to about 2000–2100 CST. This increase may be associated with high winds that began about 1130 CST and continued until about 1830–1900 CST. In the shallow waters of Baffin Bay a wind of such force stirs the water to an extent that bottom materials are well-mixed with the water.

The effect of light on the diurnal inorganic phosphate cycle is very marked as indicated in Figure 9. The data in this figure were obtained at the same station on two consecutive days; one being clear and the other being cloudy and rainy. It is suggested by these results that the smaller diurnal variation in inorganic phosphorus is due to the

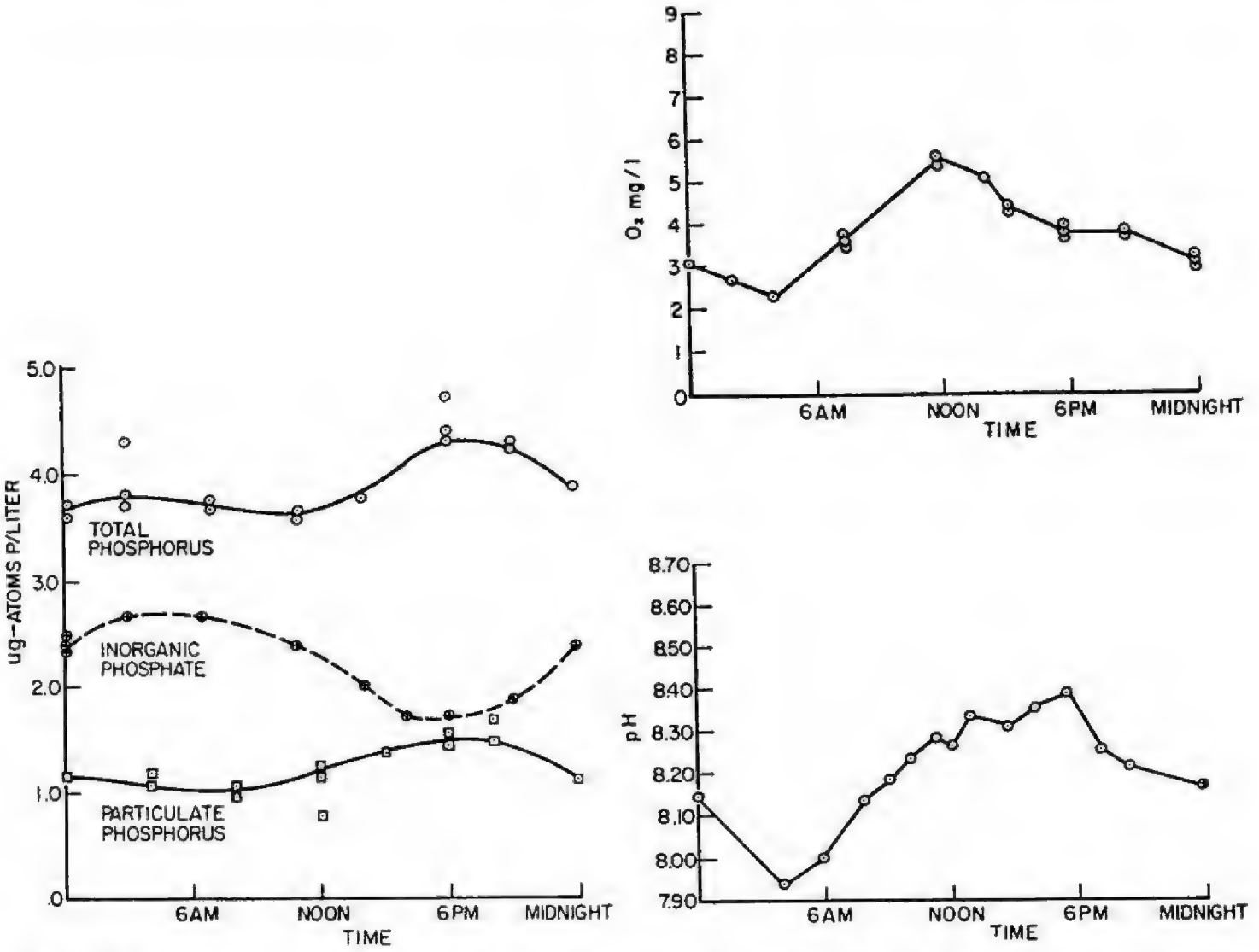


FIG. 3. Diurnal variation in inorganic phosphate, total phosphorus, and particulate phosphorus. Baffin Bay, August 1–2, 1957. Sky, clear; Wind, 15–25 mph.

FIG. 4. Diurnal variations in oxygen and pH. Baffin Bay, August 15–16, 1957.

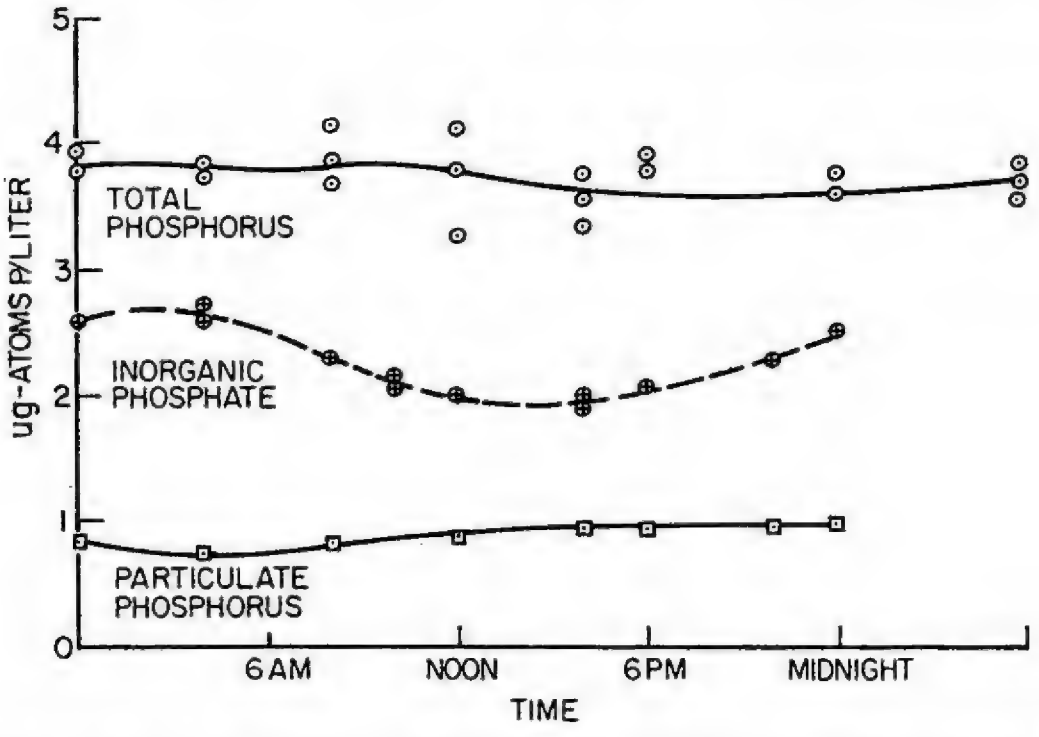


FIG. 5. Diurnal variations in inorganic phosphate, total phosphorus, and particulate phosphorus in Laguna Madre, August 1–2, 1957. Sky, clear; Wind, 10–12 mph; Salinity, 53.4 ppt.

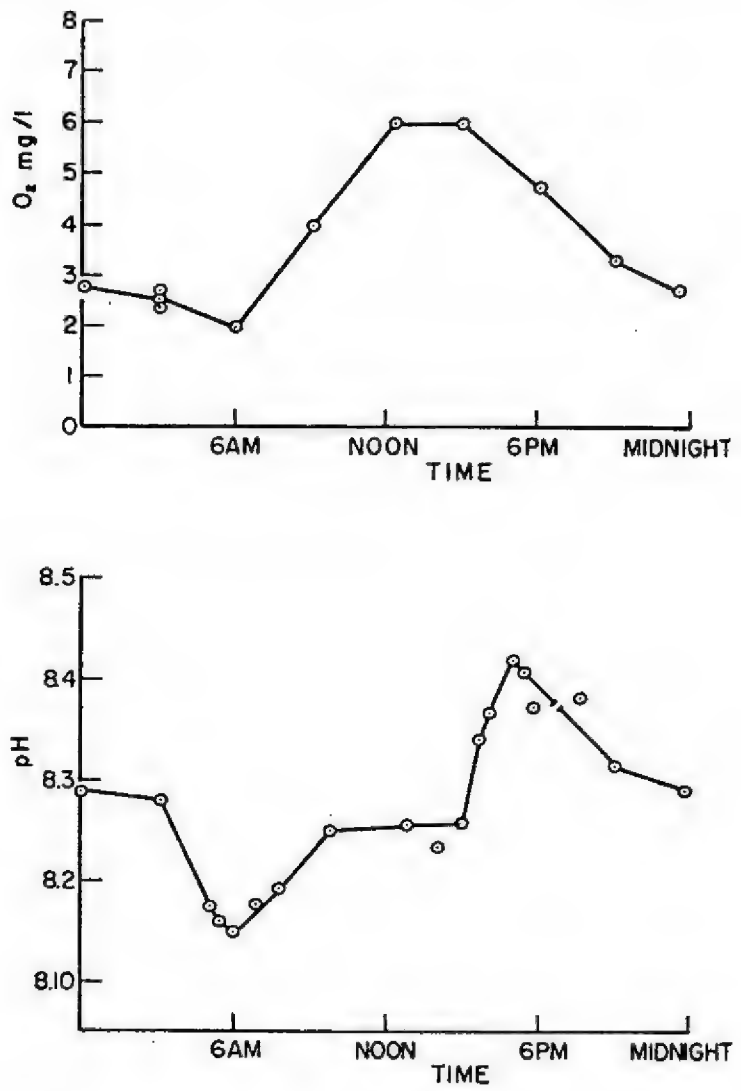


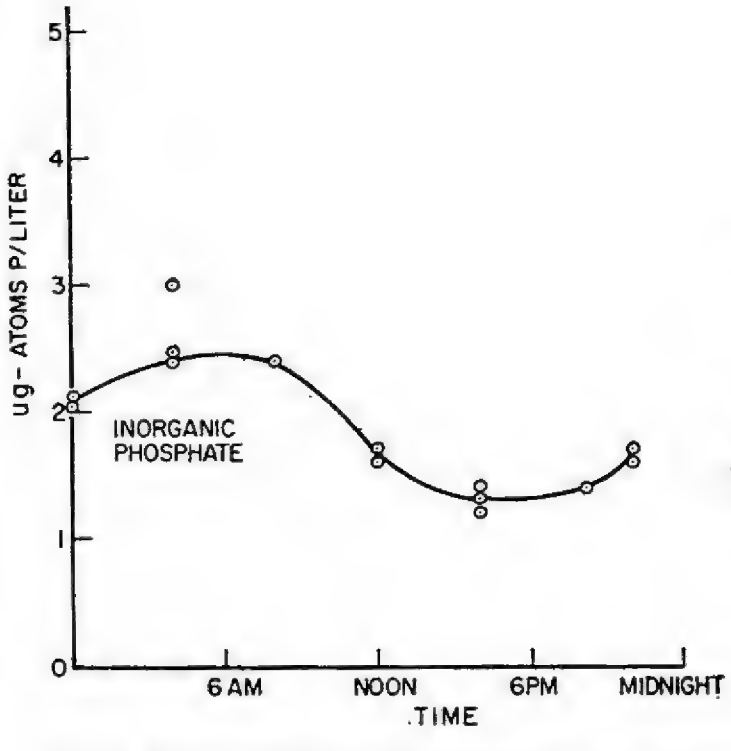
FIG. 6. Diurnal oxygen and pH variations. Laguna Madre, August 1–2, 1957.

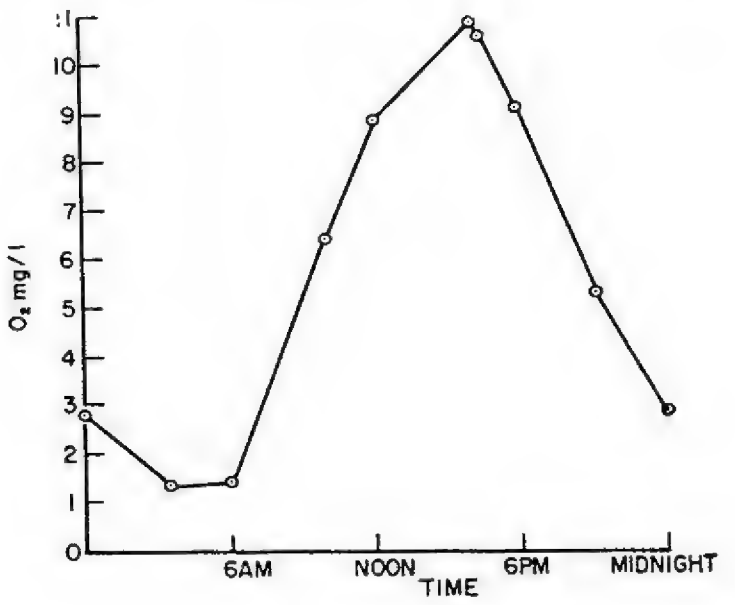
light limitation which reduced the photosynthesis in the water during the cloudy period. It is unfortunate that the oxygen and pH data were not obtained at this station in order to further verify this conclusion.

Diurnal Phosphorus Variations in Laboratory Cultures

In order to explain the causes of the variations of phosphorus in the environment studied, laboratory experiments were conducted to measure the phosphorus cycle under controlled conditions.

Experiment 1: This experiment was designed to show diurnal variation of inorganic phosphate under different population sizes and growth rates. About twelve liters of sea water were placed in each of four or five gallon carboys, and each carboy was innoculated with a mixture of *Platymonas sp.* and *Chlorella sp.* All bottles were subjected to 14 hours of lighting and 10 hours of darkness each day. After a constant population density was reached, bottles number III and IV were placed under more favorable light conditions and showed a continuous and somewhat rapid increase in population density. The first two bottles contained 10,000 to 12,000 cells per ml throughout the experiment, whereas bottle III initially contained 90,000 to 105,000 cells per ml and increased to 190,000 to 200,000 cells per ml after five days growing period. The variations of inorganic phosphate were determined by colorimetric analyses, as described previously. The results are shown in Figure 10. From the data for bottles III and IV it is apparent that





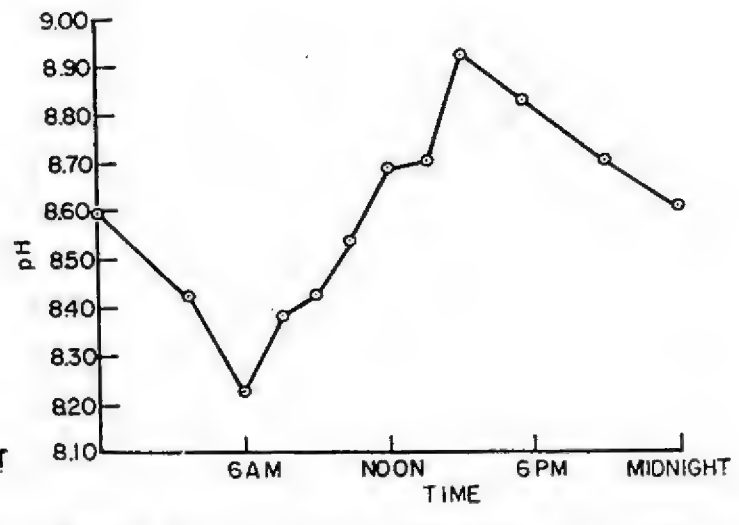


FIG. 7. Diurnal variation in inorganic phosphate at Redfish Bay, July 18–19, 1957. Sky, clear; Wind, 6–10 mph; Salinity, 30.0 ppt.

FIG. 8. Diurnal variations in oxygen and pH at Redfish Bay, July 18–19, 1957.

in densely growing populations inorganic phosphorus is produced by a combination of phytoplankton and bacterial activity in the dark and is consumed in the light. In dilute non-growing populations there is little daily change (bottles I and II).

Experiment 2: To determine the rate of release of phosphorus from dead plankton, a second experiment was conducted on the phytoplankton cultures grown in a similar fashion to bottles III and IV of Experiment 1, but with the addition of 3 millicuries of P^{32} as phosphate phosphorus. The purpose of this experiment was to measure the rate of autolytic regeneration of particulate phosphorus to inorganic phosphate by non-living material and compare this with that observed in living material. To accomplish this, three 500 ml portions of medium containing P^{32} labelled organisms were filtered through a millipore filter and were washed five times with 10 ml aliquots of distilled water. The particulate matter was then washed off the filter paper into 200 ml of artificial sea water which had been saturated with chloroform. This material was then stored at room temperature under laboratory conditions and the regeneration rate of inorganic phosphorus determined periodically by colorimetric analysis and by measuring the P^{32} content of the water.

Fifty ml samples were taken for the determination of dissolved inorganic phosphate by the method previously described. Twenty-five ml samples were taken for the total phosphorus and total dissolved phosphorus. Fifty ml samples were also filtered through

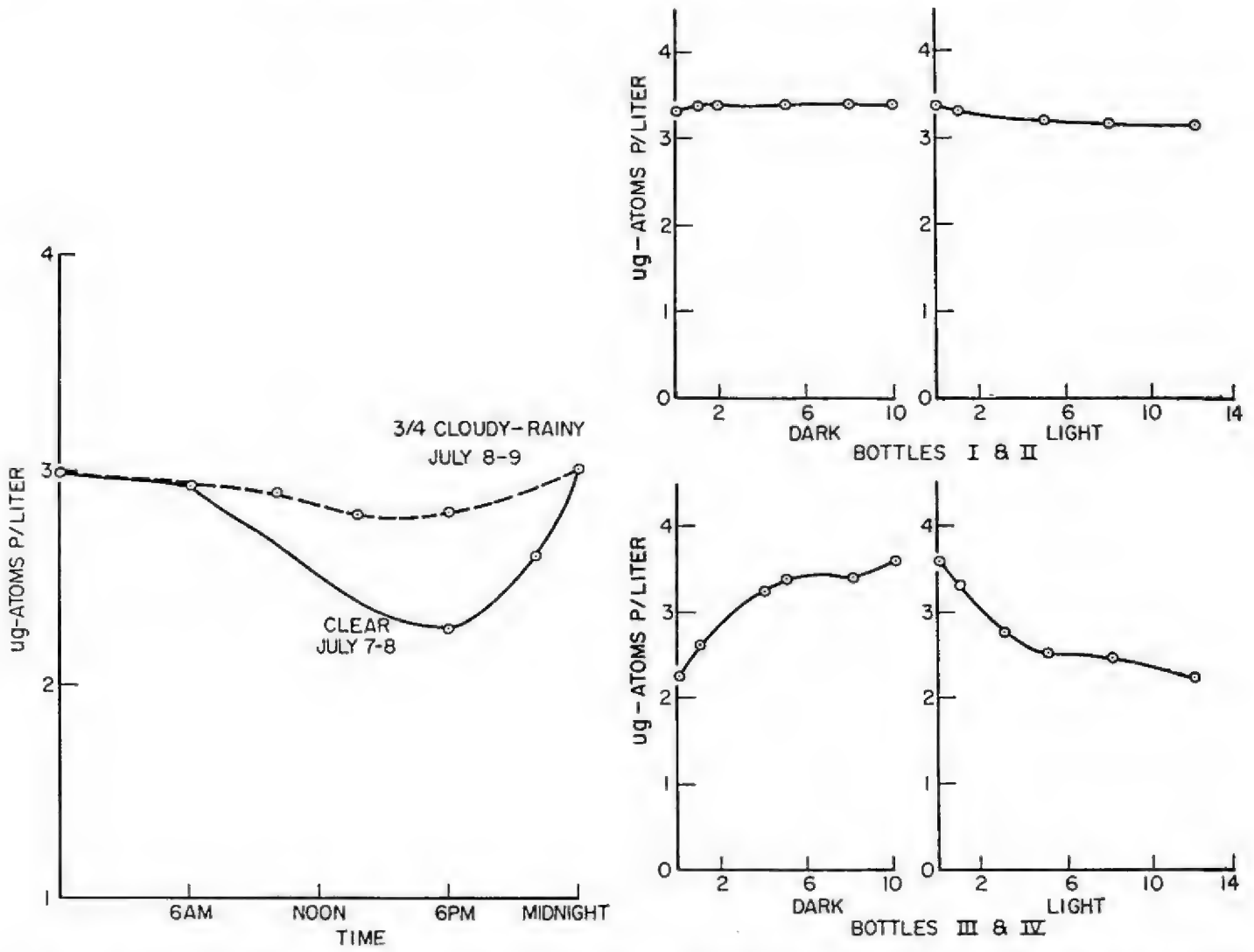


FIG. 9. A comparison between diurnal variation in inorganic phosphorus during clear and cloudy weather at Baffin Bay, July 7–8–9, 1957.

FIG. 10 Average variation in inorganic phosphorus during alternate periods of dark and illumination under laboratory conditions.

a millipore filter and the particulate material removed was washed from the filter with 25 ml of artificial sea water. This particulate material was digested and analyzed for phosphorus as previously described.

The P^{32} activity was determined with a model 182A Nuclear Chicago Gas-flow proportional counter, fitted with a D-47 counting tube and a model M-15 sample changing unit. Total activity of the water including solid material was determined on 0.5 ml samples placed in stainless steel planchets. The activity of the total dissolved phosphorus was determined by counting the filtrate from 0.5 ml samples that had passed through a millipore filter. Activity of the particulate material was determined by counting the residue remaining on the filter. All samples were run in triplicate and the results are expressed as averages of these counts. The results of this study are presented in Table 2.

TABLE 2

Regeneration of phosphorus by dead phytoplankton organisms in chloroform

	Colorimetric analysis Microgram atoms P per liter				Counts per min. per ml		
Time	Total dissolved percent	Dissolved organic percent	Dissolved inorganic percent	Particulate percent	Total	Dissolved	Particulate
Begin	44.0	3.5	41.0	53.5	10,400	600	9,800
1 hr.	51.7	9.4	45.3	.....	10,400	1,300	9,100
5 hrs.	.....	.....	.....	.....	10,400	2,400	8,000
13 hrs.	77.0	21.0	47.3	27.3	10,000	4,200	5,800
35 hrs.	.....	.....	.....	.....	10,300	6,200	4,100
48 hrs.	59.0	27.3	52.7	18.1	10,200	6,600	3,600
72 hrs.	.....	.....	.....	.....	10,200	6,700	3,500

These results show that about 35 per cent of the total phosphorus was released as dissolved organic phosphorus and inorganic phosphate in a period of 13 hours. Colorimetric analyses showed that 40 per cent of that released was inorganic and 60 per cent was dissolved organic. At the end of 48 hours, approximately 65 per cent of the total phosphorus was in the form of dissolved organic phosphorus and inorganic phosphates. Of this 65 per cent, about 80 per cent was inorganic and about 20 per cent was dissolved organic phosphorus. There was little change during the next 24 hour period.

The effect of chloroform on the hydrolysis of the organic phosphate compounds in the dead plankton is thought to be negligible since chloroform has been routinely used in isolation of caseinates, nucleanates, nucleic acid, glycerophosphates, and other well-known phosphate esters, from cellular tissue. Accepting this fact, it then appears that a great portion of the phosphate regeneration in water may arise from autolysis rather than from activity of zooplankton, phytoplankton, or the bacterial population present.

Phosphate Utilization in the Field as Traced with P^{32}

An experiment on phosphorus uptake was conducted July 7–9, 1958, in typical environmental conditions at the Baffiin Bay Station with the isotope P^{32}.

Methods

Two polyethylene bags of about 55 gallon capacity were fitted around the bottom with metal bands, one foot in diameter. The top of each bag was fitted with a rubber stopper containing a hole large enough to enable collection of water samples with a 50 ml pipet, and collection of bottom mud samples with a glass tube of about 15 mm in diameter. The metal band around the bottom was forced about six inches down into the mud bottom, thus forming a closed system. The depth of the bay at this point was three feet. Two 100 ml samples were taken for colorimetric analyses and two millicures of radioactive inorganic P^{32} were added to each bag by means of a graduated 10 ml pipet. The first sample was taken within 10 minutes after adding the P^{32}. Samples were then taken at one hour intervals for the first six hours and at four hour intervals for the next 43 hours. The samples were placed in 125 ml polyethylene bottles, frozen with dry ice, and returned to the campus laboratory. Counting techniques were used as follows:

a. To obtain total activity of water and suspended solid materials, water samples, 0.5 ml in volume were placed in stainless steel counting planchets, dried for one hour at 80°C, and counted. Samples were run in triplicate and results expressed as averages.

b. To obtain activity of dissolved materials, samples of 25 ml were filtered through a millipore filter, and 0.5 ml aliquots taken for counting. These were prepared in the same manner as described above for the determination of total activity.

c. To obtain activity of particulate material, samples of 25 ml of water were filled through a millipore filter. The filter was then washed three times with 5 ml aliquots of distilled water, and dried for 30 minutes at 80°C. The dry millipore filters were then counted, and the results expressed as the average of triplicate samples.

d. Samples of the bottom muds were taken at the same time as the water samples. Sampling was done with a six inch piece of 15 mm glass tubing held in place by means of a heavy walled rubber tubing attached to a three foot piece of 15 mm glass tubing. With the thumb clamped over the open end, the three foot piece of tubing was inserted

through the hole in the rubber stopper into the bag and extended down to the bottom mud. The thumb was then removed, and the tubing forced three or four inches into the bottom mud; the thumb was then clamped tightly over the upper end of the tubing, and the sample was removed. The six inch bottle section was removed and stoppered without disturbing the mud core. The sample was then frozen with dry ice and returned to the laboratory for analyses.

The P^{32} activity of the mud samples was determined on a 0.5 cm cross section of the core which represented the surface mud. This material was placed in 0.5 ml stainless steel counting planchets, dried in an oven at 80°C for two hours, and counted.

The activity measurements and cross sections of bottom mud beyond the 0.5 cm depth indicated that at least 90 per cent of the activity was restricted to the topmost 0.5 cm of the core.

Results of P^{32} Studies in Baffin Bay

From the data presented in Table 3 it is seen that within four hours after the addition of P^{32} to the water, there was an apparent equilibrium obtained between the phosphate absorbed on the particulate materials suspended in the water, that on the bottom muds, and that dissolved in the water. The activity of the particulate material increased for about the first three hours and then began a gradual decline. Activity of the dissolved fractions remained relatively constant after equilibration, although the P^{32}/cm^2 in the bottom mud is five to six times as great as the total P^{32} per ml of water; the total P^{32} in the water column is much greater than the total on the mud. The distribution of the P^{32} between water, particulate material, and mud is shown in Table 4. In Table 3 it may be noted that there is an obvious discrepancy between the CPM per ml of the total P^{32} in the water and CPM per ml of the dissolved P^{32} and particulate P^{32}. This discrepancy is especially noticeable in the samples taken during the first three hours after the P^{32} tracer was added. Apparently, the millipore filters on which the particulate material was retained were washed three times with 10 ml portions of distilled water, and either some

Table 3

Rate of distribution of P^{32} added to Baffin Bay

Hour of day CST	Elapsed time from start hours	CPM/ml × 10^3 total	CPM/ml × 10^3 dissolved	CPM/ml × 10^3 particulate	CPM/ml × 10^3 bottom surface	Weather
0750	1/6	12.	8.5	1.7	0.5	Calm, sky clear
0900	1	10.2	5.7	3.2	28.0	
1000	2	9.5	4.0	4.5	30.	
1100	3	7.5	3.5	4.0	34.	
1200	4	7.5	3.0	4.2	37.	
1300	5	7.3	3.0	4.0	40.	Calm, sky clear
1400	6	7.1	2.5	4.5	40.	Wind 8–10 mph
1800	10	6.9	2.6	4.2	44.	Wind 8–10 mph
2200	14	6.7	2.8	3.8	38.	Wind 5–8 mph
0200	18	6.6	3.0	3.6	40.	Calm, sky clear
0600	22	6.3	3.1	3.3	42.	Calm, sky clear
1000	26	6.4	3.0	3.3	40.	Calm, sky clear
1400	30	6.2	3.0	3.3	43.	Calm, 4/5 cloudy
1800	34	6.0	3.0	2.9	47.	
2200	38	5.8	2.9	2.8	48.	
0200	42	5.4	3.0	2.3	52.	
0600	46	5.1	3.0	2.0	58.	Wind 3–4 mph, cloudy
0900	49	5.0	2.9	2.2	62.	

CST Central Standard Time.
CPM Count per minute.

TABLE 4

Total P^{32} in each fraction of water and bottom mud

Elapsed time from start hours	Percent of total added in dissolved fraction	Percent of total added in particulate fraction	Percent of total added in bottom mud	Percent of total recovered
1/6	71	19	0.2	90.2
1	48	27	10	85
3	20	33	12	65
6	22	28	16	66
18	26	27	17	70
38	25	20	24	69
49	23	19	27	69

of the P^{32} that was absorbed on the surface of the particulate matter was washed off or cells ruptured releasing P^{32}. The counting technique did not account for the material washed off in such fashion.

Evidence for a loosely attached inorganic phosphate to particulate matter has been presented by Goldberg *et al.* (1951), in which he shows that sea water contains not only chemically bound phosphorus but also inorganic phosphate absorbed to surfaces. The data in Table 3 show that toward the end of the experiment the total P^{32} in the water is equivalent to the sum of the P^{32} in particulate and dissolved fractions. Apparently the P^{32} found in the particulate material toward the end of the experiment is chemically or physically bonded in such a fashion as not to be removed by simple washing with distilled water.

The last column of Table 4 shows that not all the P^{32} was accounted for. After a period of two hours the same percentage of P^{32} is recoverd at all time intervals. Some error may have been made in estimating the volume of the water in the bags and the total area of the bottom sediments. In addition, the geometry of the counter, as well as self-absorption, for which no corrections were made, may have varied between experimental conditions and initial conditions. Also, activity of P^{32} was found in the mud down to approximately 1.5 cm although only the top 0.5 cm was used for assay.

Despite the above discrepancies, it is felt that the preliminary picture of the distribution of P^{32} added to the water is correct.

General Discussion of Phosphorus Cycle

The results obtained from these studies show that diurnal changes in concentration of inorganic phosphate do occur in the bays of South Texas. Although considerable variations were found to exist between the different environments studied, there seems to be a general agreement as to the occurrence of low concentrations of inorganic phosphate during the daylight hours, and a corresponding higher concentration at night.

The laboratory experiments indicate that the greatest diurnal variation of inorganic phosphate occurs in heavy populations of phytoplankton undergoing rapid growth. Only with relatively light, non-growing populations with activity limited to community maintenance was there little variation of inorganic phosphate. These results do not conflict with conclusions drawn by Pratt (1950) that the rate of regeneration of phosphate is determined by the size of the standing crop while the utilization rate of inorganic phosphate is determined by the growth rate of the phytoplankton.

The diurnal variations observed during these experiments are apparently due to the

increased utilization of inorganic phosphate by the phytoplankton during the periods of lumination. The regeneration process in rapidly multiplying cells probably continues at all times, and the fluctuation in phosphate concentration is an indication of the difference between the regeneration rate and the rate of utilization, a phenomenon not dissimilar to respiration and photosynthesis in these same plants.

In the laboratory experiments the regeneration must have been derived from bacterial action, autolysis, and metabolism within the plants themselves, since no animal population existed in these experiments. Remineralization of phosphorus from dead phytoplankton in chloroform indicates that regeneration of phosphorus by autolytic processes is rapid enough to account for some of the observed diurnal variation in the environment studied. This thesis is not free of difficulties, however, for the effect of chloroform on enzymatic processes involved in phosphorus regeneration is unknown, and chloroform action on the phytoplankton cell membranes may have caused normally retained phosphorus to be excreted into the water solution where it was detected by the analytical method employed. More information is needed on the nature of the phosphorus compounds excreted by organisms and existent in free solution in the environment.

The possibility exists that the diurnal variation of wind could be a contributing factor to variation of inorganic phosphate. The diurnal phosphorus variation might be due to the daily variation of the water mixing with the sediment. If inorganic phosphorus were absorbed by the particulate matter during strong winds, it might settle out when the wind lessened, thus giving a diurnal effect. However, this effect cannot be the major cause, since the diurnal effect was shown on several occasions when the water was relatively calm.

When P^{32} was added to the polyethylene bag in Baffin Bay an equilibrium was reached between the P^{32} in the water, on the particulate matter, and on the bottom mud within three hours, with better than 20 per cent of the P^{32} lost to the bottom muds. The loss from the water for the next 47 hours was more gradual finally resulting in about 70 per cent of the P^{32} in the sediment phase after 49 hours. If the rate of loss of P^{32} from the water to the mud continued at the same rate as during the study period, practically all of the P^{32} would be removed from the water in six to eight days.

However, the concentration of dissolved phosphorus remained constant during the last 45 hours of the experiment, whereas the P^{32} of the particulate matter decreased. The P^{32} increase in the bottom muds probably results both from absorption and the settling out of particulate matter. The fact that the dissolved fraction remains nearly constant while the sediments increase and the particulate material decreases indicates dynamic exchange of dissolved organic and inorganic phosphorus between the sediment, particulate material, and dissolved phosphorus in the water. These data support the conclusions of Coffin *et al.* (1949), Hayes *et al.* (1951–52), and Hutchinson and Bowen (1947), regarding an active exchange between dissolved phosphorus and the phosphorus present in solid material and bottom sediments. The previous works indicated a complete turnover rate of about 14 days for phosphorus. The results of this study indicate a turnover rate of between 10 and 20 days. Due to the shallow water and wind effect in Baffin Bay, the turnover rate may vary considerably.

The strong correlation between diurnal variation in inorganic phosphate and primary production as measured by diurnal pH and oxygen variation suggests the possibility of using the diurnal phosphate cycle as a means of estimating primary production. There is evidence, however, that primary production can be maintained under certain conditions

by certain dissolved organic phosphorus compounds. Also, the rate of regeneration of inorganic phosphate is dependent to a large extent upon population size; hence, the absence of a diurnal variation of inorganic phosphate may not necessarily indicate an absence of primary production at a significant rate. Pronounced diurnal variation in inorganic phosphate in the areas investigated by this study was accompanied by a high rate of primary production. It appears that if a pronounced diurnal variation of inorganic phosphate is found, primary production is occurring at a significant rate. Under these conditions, the diurnal variation in inorganic phosphate may be useful in primary production considerations.

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Plankton Productivity in Estuarine Waters of Georgia[1]

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Abstract

Primary production of the plankton community in the estuarine waters near Sapelo Island, Georgia was estimated by oxygen evolution in light and dark bottles at several locations. Data on temperature, light, and chlorophyll *a* were obtained for most of the experiments. The average gross production by plankton was +0.68 gm C/m²/day, and net planktonic community production averaged —0.038 gm C/m²/day. The plankton community tended to be heterotrophic in the summer and autotrophic in the winter. The primary factor limiting production was light. Analysis of compensation depths and extinction coefficients shows that for the mean depth of these waters and under the observed conditions of light and vertical mixing, net production by the plankton community must be near zero regardless of the standing crop. The salt marsh is postulated as an outside source of organic matter of the system.

Introduction

Estuaries in general are considered to be more productive at the primary level than coastal or offshore waters. This generalization tends to be supported by available data (Odum and Hoskin, 1958) although there are very few published records of direct measurements of primary productivity in estuaries. Marshall (1956) has summarized chlorophyll data from various sources showing that chlorophyll levels tend to be higher in estuaries than in either coastal or slope water. The work of Riley *et al.* (1949) indicates that productivity in Long Island Sound, which might be considered an estuary, is usually higher than in coastal waters.

Preliminary reports by Thomas, Simmons, and Corcoran (1957) on the waters of the Mississippi Delta indicate that phytoplankton productivity in those waters is high but variable. The measurements were made by the C^{14} method which, according to Ryther (1956a), tends to measure net production rather than gross production by the phytoplankton. Thomas *et al.* obtained average production rates of 738 and 891 mg C/m²/day for two different areas of which they calculate 85 per cent might eventually reach the sediments. They also conclude "that light is a principal limiting factor in these waters."

On first observation of the estuarine waters around the sea islands of Georgia one is immediately impressed with the brown color and obviously slight penetration of light. This highly turbid water extends from the mainland through the various interconnecting tidal channels and sounds, and offshore for a distance of two to nine miles. A final line of demarcation between slightly turbid shore water and relatively clear coastal water lies more or less parallel to the coast about 10 to 15 miles offshore. The effect of the turbidity on phytoplankton photosynthesis is undoubtedly important in regulating plankton pro-

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ductivity. The question arises whether plankton production may not be severely reduced by this turbidity. It is primarily to this question that this paper is addressed.

A brief description of the sea island region is given by Galtsoff and Luce (1930) and Ragotzkie and Bryson (1955). For the present work it will suffice to mention that a five to seven mile wide complex of water and salt marsh lies between the mainland and the sea islands. This is composed of salt marsh irrigated by a network of sounds, tidal rivers, and creeks (Figure 1). The tide has a mean range of 6.8 feet (2.06 m) and a spring range of 8.0 feet (2.42 m). The water is fairly shallow, nearly all of it being less than 10 meters deep. As a result, the turbulent flow during the ebb and flood of the tide, stirs up the unconsolidated sediments thus maintaining a high degree of turbidity most of the time. Salinity varies with the nearness of the fresh water rivers (the Altamaha, the Ogeechee, and the Savanah) and with the rainfall. In most of the region the salinity ranges from 20 to 30 ppt.

Methods

Production and Respiration

Estimates of primary planktonic production were made by measuring changes in dissolved oxygen in light and dark bottles (Gaarder and Gran, 1927). The validity of this method has been discussed by Steeman-Nielsen (1952), Ryther and Vaccaro (1954), Vaccaro and Ryther (1954), and Ryther (1956a). It appears from these studies of the method that although it is not ideal, it is reasonably good provided the experiments are not of excessive duration. The following experiments were all of 24 hours duration.

One of the main objections to the light-dark bottle method is that the increased surface provided by the bottle may give rise to excessive bacterial growth and that consequently respiration may be overestimated. The significance of this effect was investigated by the following experiment. Surface water collected from the Duplin River was placed in dark citrate bottles and suspended in the river; thus, no temperature change was imposed, constant temperature conditions were maintained, and the degree of agitation was the same as that for the light-dark bottle experiments. Dissolved oxygen content of the water was determined for three bottles at six-hour intervals for 33 or 36 hours (Figure 2). If bacterial growth had been increased by enclosure in the bottles, greater respiration might have been observed in the bottles submerged for longer time. The linearity of the oxygen uptake suggested that bacterial growth was not interfering with the total respiration estimate.

In field experiments, water was pumped, from one or two levels, and siphoned into citrate bottles which were then incubated at 0.5, 2, and 4 meters. Respiration rates were found in most cases to be constant with respect to depth so that three levels were enough. That respiration was constant with depth is not surprising since vertical mixing by tidal circulation effectively prevents prolonged stratification. Temperature measurements made at the start of each experiment showed that the water column was either isothermal or had a total temperature gradient of 1°C or less. Chlorophyll measurements (Tables 1, 2, and 3) also indicated little stratification.

Dissolved oxygen was determined by the Winkler method. Where blooms existed the Pomeroy-Kirschman sodium azide modification was used to avoid errors due to excessive organic matter (APHA, 1955). The changes in the dissolved oxygen content of the water in the bottles were plotted against depth and the resulting curves integrated with

respect to depth to obtain changes on an areal basis. Compensation depth, D, was taken as the level at which the curve of rate of oxygen change in the light bottle reached zero. The mean depth of the water within one tidal prism of the station was used as the lower depth limit in the computations on the dissolved oxygen curves. Net production of the plankton community (including detritus and bacteria) is defined as photosynthesis

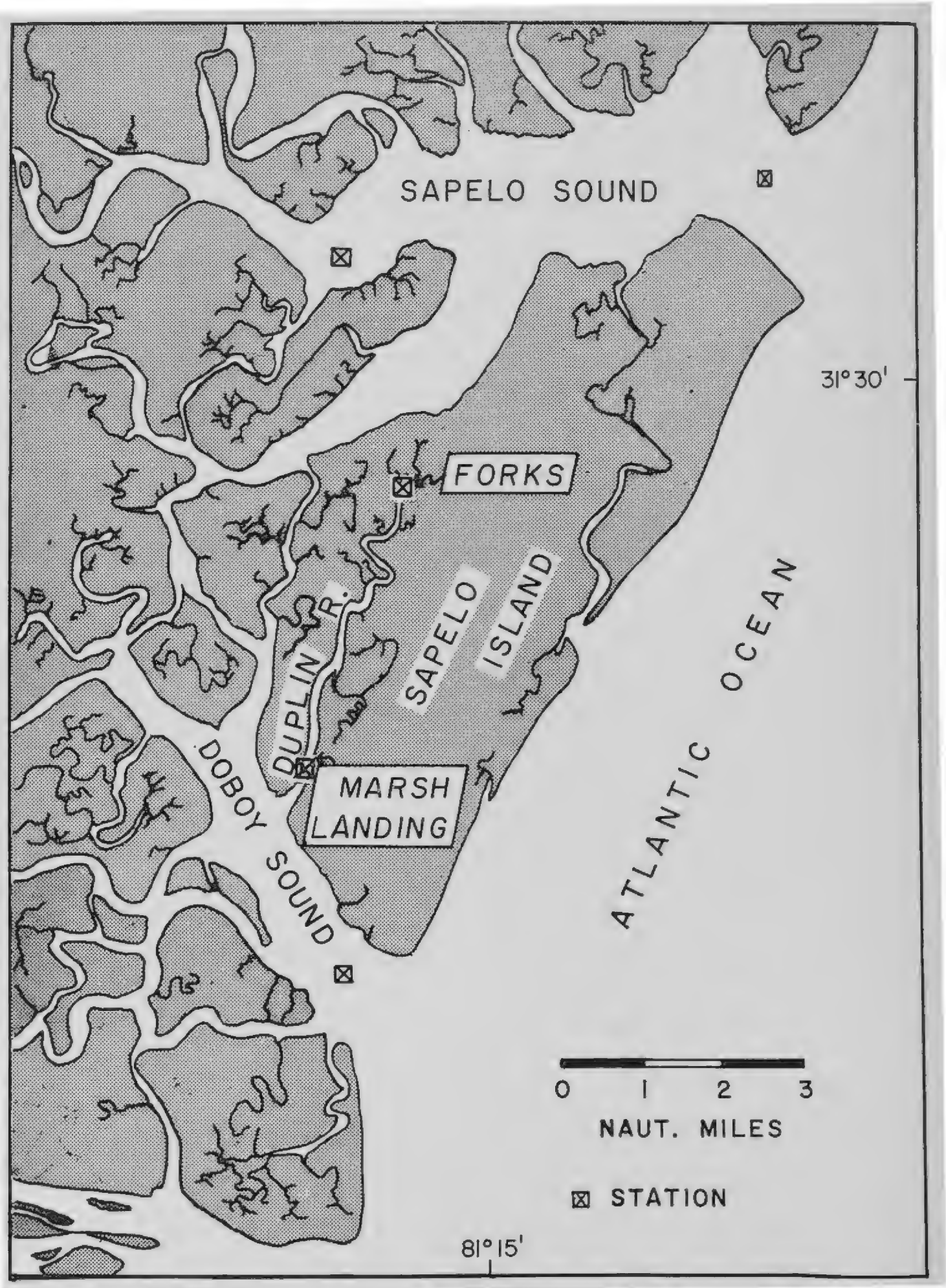

FIG. 1. Map of Sapelo Island, Georgia, and adjacent waters showing location of stations.

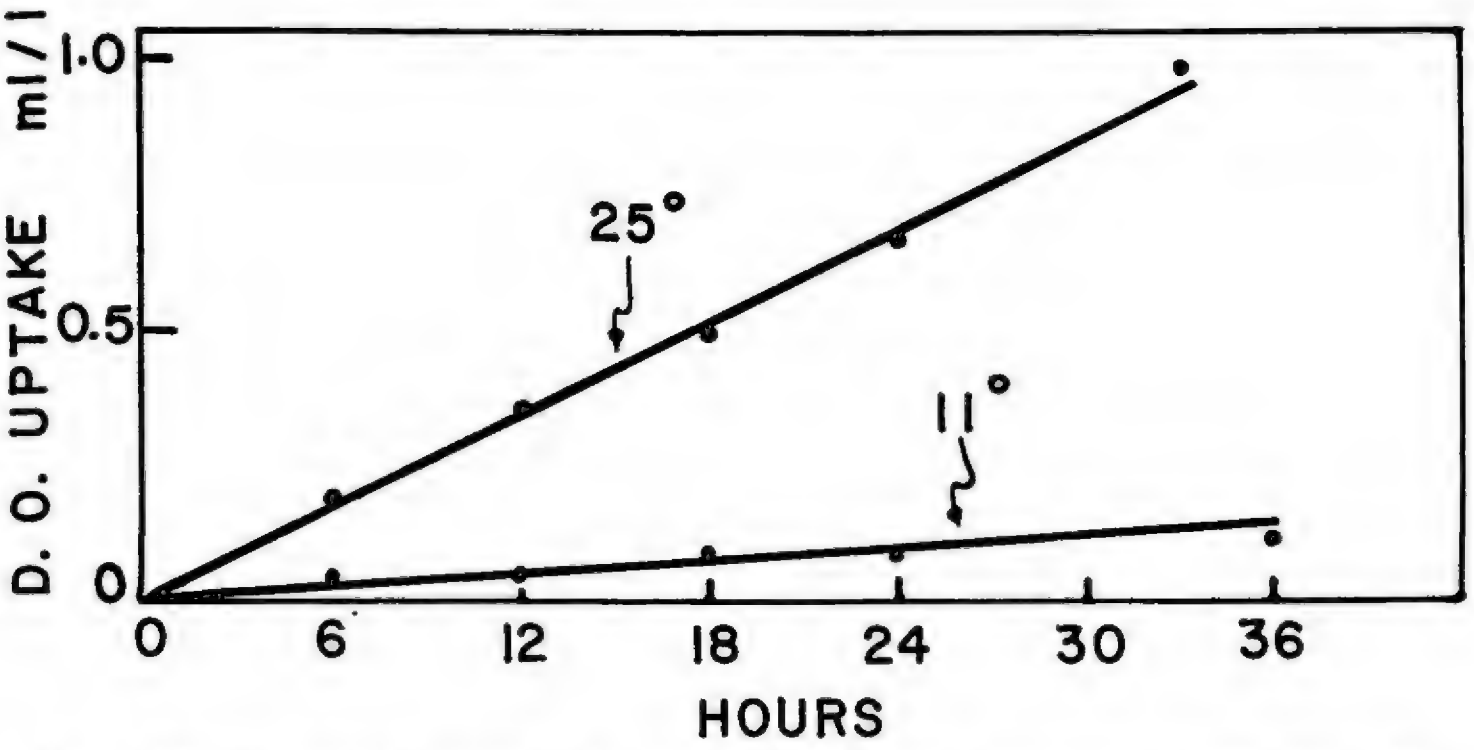

FIG. 2. Rate of dissolved oxygen (D.O.) uptake in dark bottles suspended in Duplin River. Each point represents the mean of 3 bottles.

minus respiration of the plankton community, and it is estimated from the area enclosed by the light bottle curve. Where dissolved oxygen changes are negative, the area is taken as negative. Gross production is total photosynthesis and is estimated algebraically by adding the areas under the light and dark bottle curves. Results were converted to grams carbon fixed/m^2/day using a photosynthetic quotient of 1.25 (Ryther, 1956a).

Diurnal oxygen curves for the Duplin River were obtained by the following procedure. A free drag was used to follow a parcel of water during its excursion in the tidal prism extending upstream (flooding tide) from Marsh Landing. Water samples were collected near the drag at frequent intervals from two or three levels from the surface to near the bottom and the dissolved oxygen content determined in triplicate at each depth. As previously indicated vertical mixing effectively prevents stratification with respect to temperature or chlorophyll. As might have been expected, dissolved oxygen was also practically constant with depth; therefore the results of each series were averaged and the mean values used to construct the curves.

CHLOROPHYLL

Chlorophyll was estimated by the spectrophotometric method of Richards with Thompson (1952) using the Millipore Filter modification of Creitz and Richards (1955). Chlorophyll was estimated for only one-quarter of the experiments.

TEMPERATURE

Water temperature was measured with the Whitney Underwater Thermistor Thermometer.

LIGHT

Light transmission was measured with an underwater densitometer (photometer). A brief description of this instrument is given by Ragotzkie and Pomeroy (1957). It was found that the extinction coefficients, $k_{tungsten}$, as obtained with this instrument were consistently higher than those obtained with an underwater light meter activated by

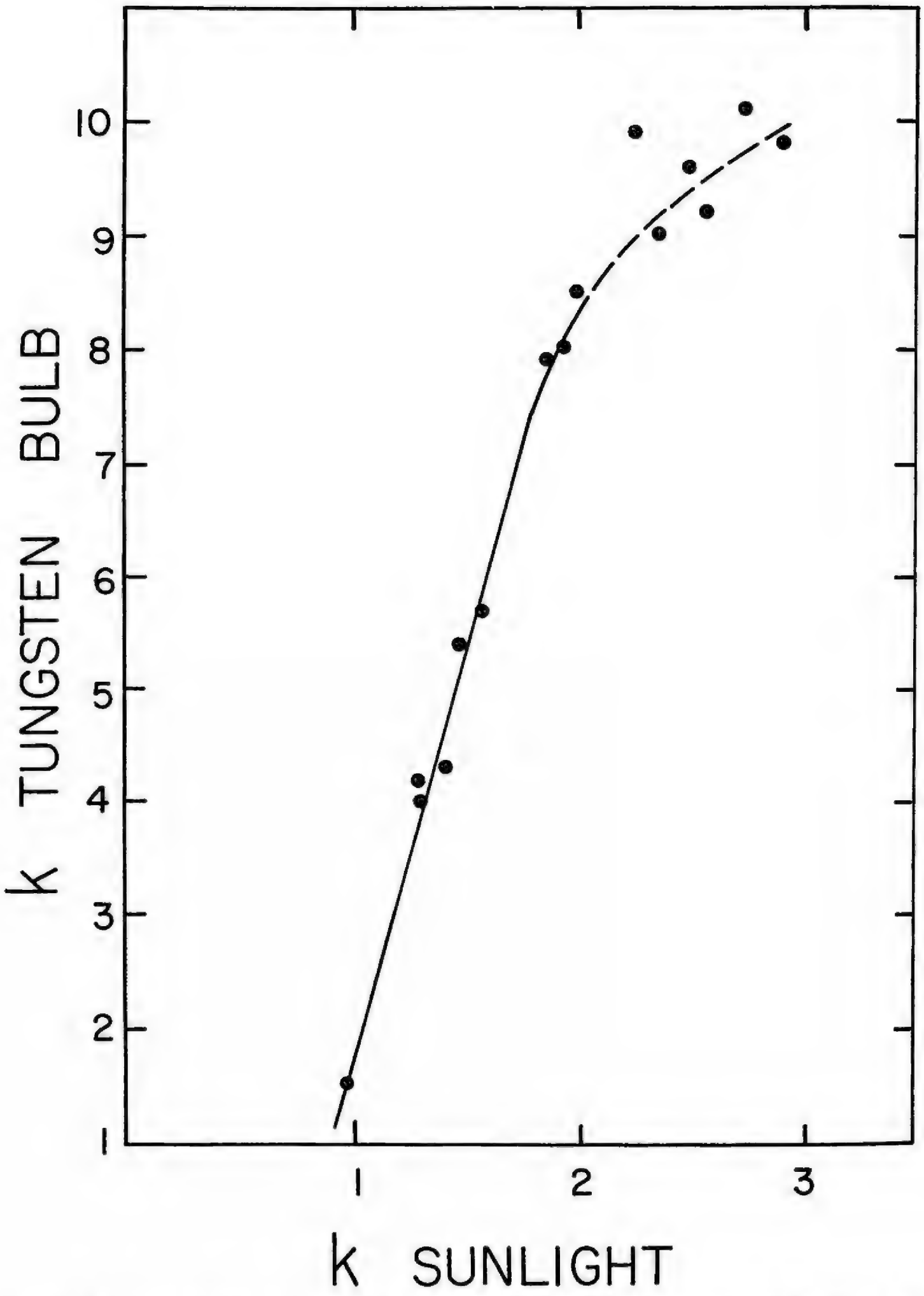

FIG. 3. Relation between extinction coefficient obtained with Whitney densitometer, $k_{tungsten}$, and coefficient of sunlight, k_{sun}. Both k's are expressed per meter. The densitometer has a collimator in the light path, thus, reducing the scatter acceptance and reducing the observed transmission. The resulting curve shows the empirical relationship between the two extinction coefficients.

sunlight alone. In order to obtain k_{sun} values for sunlight, simultaneous measurements were made with both instruments under various conditions of turbidity. The two sets of k values were then plotted against each other (Figure 3) and the extinction coefficients for sunlight determined directly from this curve.

This somewhat involved procedure was adopted because light intensity below two or three meters in these waters is generally so low that a sunlight activated underwater meter loses much of its sensitivity while the densitometer, having a fixed light path, permits rapid and accurate measurements at all depths. Furthermore, the turbidity varies sharply with depth, and the sunlight activated meter indicates this in only an approximate way.

The majority of the experiments were conducted in the Duplin River, a tidal river receiving no freshwater run-off. A few measurements were made in the two sounds adjoining Sapelo Island (Figure 1). Nearly all experiments were started at either high or low slack water.

Seasonal Pattern of Productivity

Experimental data are summarized in Tables 1, 2, and 3. Temperatures reported are means of the temperatures of the water column at the beginning and end of the experiment. Extinction coefficients are also average values.

The seasonal pattern of productivity is shown in Figure 4 where the net and gross production rates have been plotted in a bar graph. A curve of mean water temperature has

TABLE 1

Production data for Marsh Landing, Duplin River, mean depth, 4.6 meters

Date	Tide at start	Respiration gm C/m²/day	Net production gm C/m²/day	Gross production gm C/m²/day	Temperature °C	Extinction coefficient /m	Compensation depth in m	Critical depth in m	Chlorophyll *a* in mg/m³	
Jan. 20, 1955	low	0.20	+0.43	0.63	10.5	.....	2.15	.....	.....	.....
Apr. 5, 1955	low	0.73	+0.22	0.95	17.5	.....	3.25	.....	.....	.....
Apr. 12, 1955	high	0.31	+0.46	0.77	19.0	.....	2.00	.....	.....	.....
Apr. 18, 1955	high	0.67	+0.46	1.13	22.5	.....	2.00	.....	.....	.....
May 3*, 1955	low	1.27	−0.42	0.85	22.2	.....	1.35	.....	.....	.....
May 4, 1955	low	0.56	+1.17	1.73	22.5	.....	3.25	.....	.....	.....
May 18, 1955	low	1.19	−0.69	0.50	24.5	.....	0.00	.....	.....	.....
June 13, 1955	high	0.80	−0.46	0.34	25.5	.....	0.00	.....	.....	.....
June 14, 1955	low	0.55	−0.11	0.44	25.5	1.40	1.25	4.1	.....	.....
June 15, 1955	high	0.71	−0.28	0.43	25.4	3.00	2.20	12.0	.....	.....
June 30*, 1955	high	1.25	−0.43	0.82	26.8	2.58	1.22	9.2	.....	.....
July 12, 1955	high	1.40	−0.70	0.70	29.0	2.22	0.70	2.1	.....	.....
July 12, 1955	low	0.98	−0.65	0.33	29.3	1.25	1.00	2.8	.....	.....
July 27, 1955	high	1.00	−0.30	0.70	29.5	1.44	1.65	7.5	.....	.....
Aug. 31, 1955	high	0.76	+0.21	0.97	29.5	3.50	1.65	93.	.....	.....
Oct. 13, 1955	low	0.67	−0.13	0.54	24.0	3.00	1.15	11.	.....	.....
Oct. 27, 1955	low	0.41	+0.18	0.59	20.0	1.42	1.75	8.5	.....	.....
Oct. 27, 1955	high	0.30	+0.24	0.54	20.7	2.34	1.75	26.	.....	.....
Dec. 9, 1955	high	0.25	+0.09	0.34	13.5	2.30	2.00	43.	.....	.....
Jan. 30, 1956	high	0.0	+0.47	0.47	10.2	.....	2.50	.....	.....	.....
Feb. 13, 1956	low	0.23	+0.19	0.42	15.0	1.63	2.00	16.	10.0†	8.8
Feb. 17, 1956	low	.....	.....	0.10	17.5	1.46	0.0	0.68	5.2	6.4
Apr. 18, 1956	low	0.37	+0.18	0.55	18.0	1.38	2.40	20.	7.8	6.4
May 14, 1956	high	0.55	−0.03	0.52	24.2	2.45	1.75	30.	18.6	23.1
July 4, 1956	low	1.15	−0.29	0.86	28.0	1.50	1.40	5.5	19.8	17.1
July 23, 1956	low	0.72	+0.16	0.88	29.5	1.68	1.75	11.	15.5	.....
Oct. 4, 1956	low	2.22	−0.96	1.26	25.5	1.32	1.10	3.2	.....	.....

* Mean of duplicate experiments.
† Where two values are given, one is for one meter depth and the second for a level near the bottom.

TABLE 2

Production data for forks, mean depth low water 2.8 meters, high water 4.8 meters

Date	Tide at start	Respiration gm C/m²/day	Net production gm C/m²/day	Gross production gm C/m²/day	Temperature °C	Extinction coefficient /m	Compensation depth in m	Critical depth in m	Chlorophyll *a* in mg/m³	
Feb. 17, 1955	high	0.20	+0.14	0.34	.....	0.88	2.45	9.9	.....	.....
*March 1, 1955	low	6.2	+16.4	22.6	18.0	1.15	2.70	20.	.....	.....
*March 2, 1955	half	0.65	+0.25	0.90	18.3	1.26	2.00	9.9	.....	.....
*March 3, 1955	half	0.50	+0.59	1.09	19.5	1.25	1.70	6.8	.....	.....
March 30, 1955	high	.....	+0.40	.....	13.5	1.17	3.10	32.	.....	.....
Apr. 5, 1955	half	0.42	−0.05	0.37	18.0	.....	0.75	.....	.....	.....
May 4, 1955	low	0.40	+0.50	0.90	22.2	.....	2.20	.....	.....	.....
May 18, 1955	low	0.69	+0.05	0.74	24.8	.....	1.75	.....	.....	.....
June 13, 1955	high	0.70	−0.01	0.69	26.4	.....	1.70	.....	.....	.....
July 12, 1955	high	2.34	−2.28	0.06	30.0	1.30	0.0	0.77	.....	.....
July 12, 1955	low	0.92	−0.90	0.02	29.9	1.49	0.0	0.67	.....	.....
Dec. 9, 1955	high	0.22	0.00	0.22	12.5	1.15	2.25	12.	.....	.....
Jan. 31, 1956	high	0.20	+0.04	0.24	12.2	1.19	1.65	6.0	.....	.....
March 17, 1956	low	0.62	−0.35	0.27	17.6	1.30	0.0	0.77	2.6	.....
Apr. 18, 1956	low	0.33	+0.29	0.62	18.0	1.46	2.25	18.	†8.1	6.8
July 4, 1956	low	1.39	−0.61	0.78	28.2	1.36	0.0	0.73	22.2	.....
July 23, 1956	low	2.40	−0.23	2.17	30.5	1.62	1.10	3.7	27.7	.....
Oct. 4, 1956	low	0.66	+0.54	1.20	27.0	1.48	1.90	11.	.....	.....

* Dinoflagellate bloom.
† First value for one meter depth, second value for three meters depth.

TABLE 3

Production data for stations in the sounds

Date	Station	Respiration gm C/m²/day	Net production gm C/m²/day	Gross production gm C/m²/day	Temperature °C	Extinction coefficient /m	Compensation depth in m	Critical depth in m	Chlorophyll *a* in mg/m³	
Apr. 12, 1955	Doboy Sound	0.51	+1.07	1.58	19.5	.....	4.00	.....	.....	.....
Apr. 18, 1955	Doboy Sound	0.91	+0.37	1.28	20.0	.....	.....	.....	.....	.....
Feb. 13, 1956	Sapelo Sound mouth	0.24	+0.22	0.46	13.0	1.56	1.75	9.9	*6.8 4.7	5.1
Feb. 13, 1956	Sapelo Sound landward	0.47	−0.14	0.33	14.8	1.62	1.85	12.	5.8	7.1
May 14, 1956	Sapelo Sound landward	0.34	+0.20	0.54	23.8	1.59	3.00	74.	.....	.....

* First value for one meter and others for deeper levels.

been entered on the same plot. For the Marsh Landing station it is apparent that during the summer net production tends to be low or negative while gross production remains about the same. This difference appears to be due to a strong increase in bottle respiration during the summer season with no corresponding increase in photosynthesis. There are fewer data for the Forks station, but the trend appears to be similar. It should be pointed out that the plankton includes organic detritus and its associated bacterial flora. Organic detritus concentrations, though variable, usually exceed 1 mg/l.

A more precise way of demonstrating the metabolic characteristics of the plankton community is afforded by the P-R diagram (Odum, 1956) in which gross photosynthesis is plotted against respiration. A P/R ratio of one is the dividing line between auto-

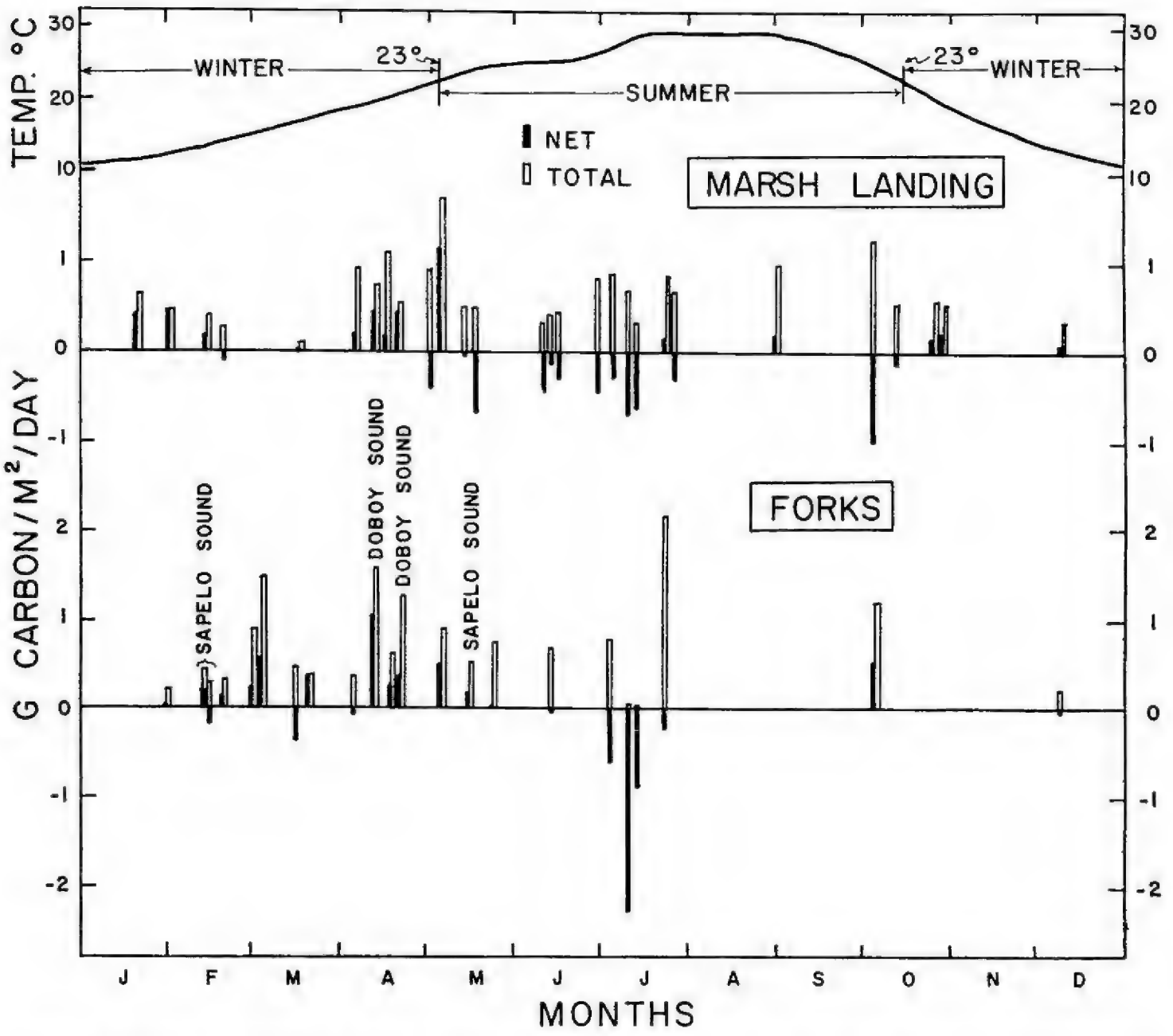

FIG. 4. Results of light-dark bottle experiments together with the average water temperature curve. Black bars are rates of net production of the plankton community in the bottles (changes in the light bottle); unshaded bars are rates of gross production of the phytoplankton (sum of light and dark bottle changes).

trophy and heterotrophy of the community. By plotting the present data on a P-R diagram a seasonal separation appears (Figure 5). Defining the seasons on the basis of this separation one finds that during the winter, October 16-May 5, the P/R ratios are nearly all greater than one, indicating autotrophy, while during the summer, May 6-Oct. 15, the ratios are less than one, indicating heterotrophy. Although the points are scattered, it appears that this change in community trophic type is brought about by an increase in respiration rather than any change in photosynthesis.

The summer season as defined by the trophic characteristics also coincides with that period when the mean temperature of the water is 23°C or above (Figure 4). Thus, above 23° the system tends to be heterotrophic while below 23° the tendency is toward autotrophy. One possible reason for this is that the rate of photosynthesis is relatively insensitive to temperature while respiration increases with temperature. Barker (1935) found photosynthesis by diatoms is practically independent of temperature at low light intensities. Wassinck and Kersten (1944) reported that below a light intensity of 0.015 cal/cm²/min. temperature had no effect on photosynthesis by two marine diatoms. In the waters near Sapelo Island, solar radiation does not exceed this value except in the upper one to two meters during peak hours in mid-summer. Steeman-Nielsen and Hansen

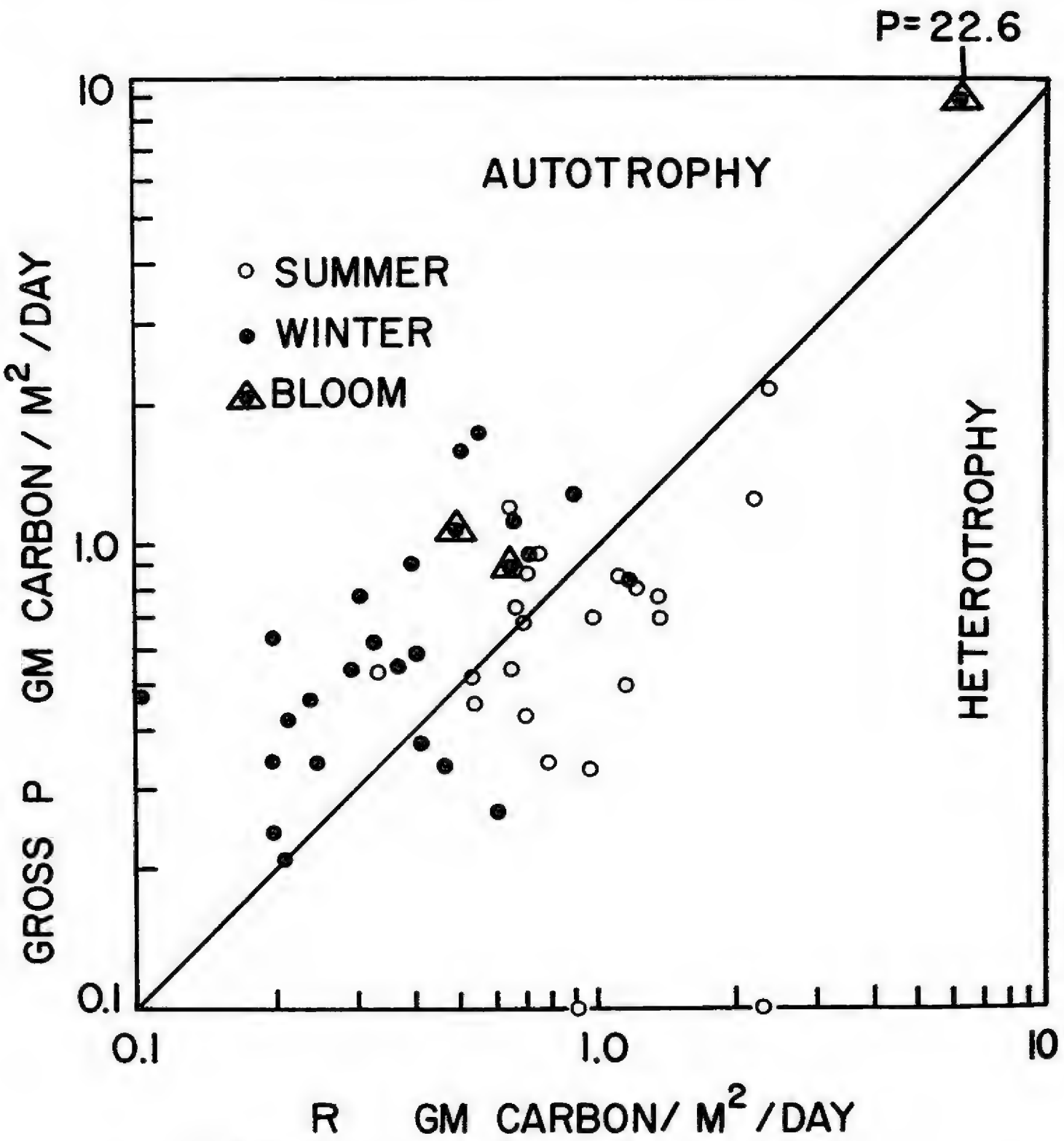

FIG. 5. P/R diagram for results of all light-dark bottle experiments.

(1959) also found that photosynthesis by natural populations of phytoplankton is "moderately independent of temperature."

However, respiration by most plankton organisms tends to increase with temperature. Some species adjust to temperature changes, maintaining a nearly constant respiration rate, while in others the respiration rate increases with temperature. The net effect, therefore, is an increase in community respiration with temperature (Riley *et al.*, 1949). Furthermore, bacteria, of which there are up to 25,000/ml in these waters, may be expected to increase their respiration rate with temperature. Thus a rise in temperature will, in itself, tend to push the system toward heterotrophy.

The standing crop of phytoplankton may also be expected to have an effect on the P/R ratio. The available chlorophyll values, are all higher in the summer than in the winter. Coupled with higher incoming radiation in the summer, this higher standing crop of chlorophyll might be expected to result in a higher rate of gross photosynthesis.

Why none occurs cannot be explained. The phosphate and total phosphorus supply is better in the summer than in the winter (Pomeroy, personal communication).

Two diurnal oxygen curves were determined for the Duplin River (Figure 6). In both cases the water remained undersaturated with oxygen during the entire 24 hours despite obvious photosynthetic activity. Reaeration was also undoubtedly significant since tidal currents provide ample mixing. The implication is that respiration exceeded photosynthesis. It must be pointed out that changes in dissolved oxygen in the entire river are brought about by the combined processes of plankton photosynthesis and respiration, benthic respiration, photosynthesis of algae on the mud surface of the intertidal mud and marsh, and by diffusion. In the Duplin River the intertidal area may be one to five times the area of the river itself depending on the height of high water (Ragotzkie and Bryson, 1955). Since the surface area of the water and the bottom varies with the tide, the various processes affecting the oxygen concentration could not be evaluated separately by the method of Odum (1956). Production by algae on the mud surface of the intertidal area has been shown to be quite high (Pomeroy, 1959). As mentioned above, diffusion could only act in the direction of increasing oxygen concentration. Therefore, the consistent oxygen undersaturation can be regarded as additional evidence for high respiration rates by the planktonic community.

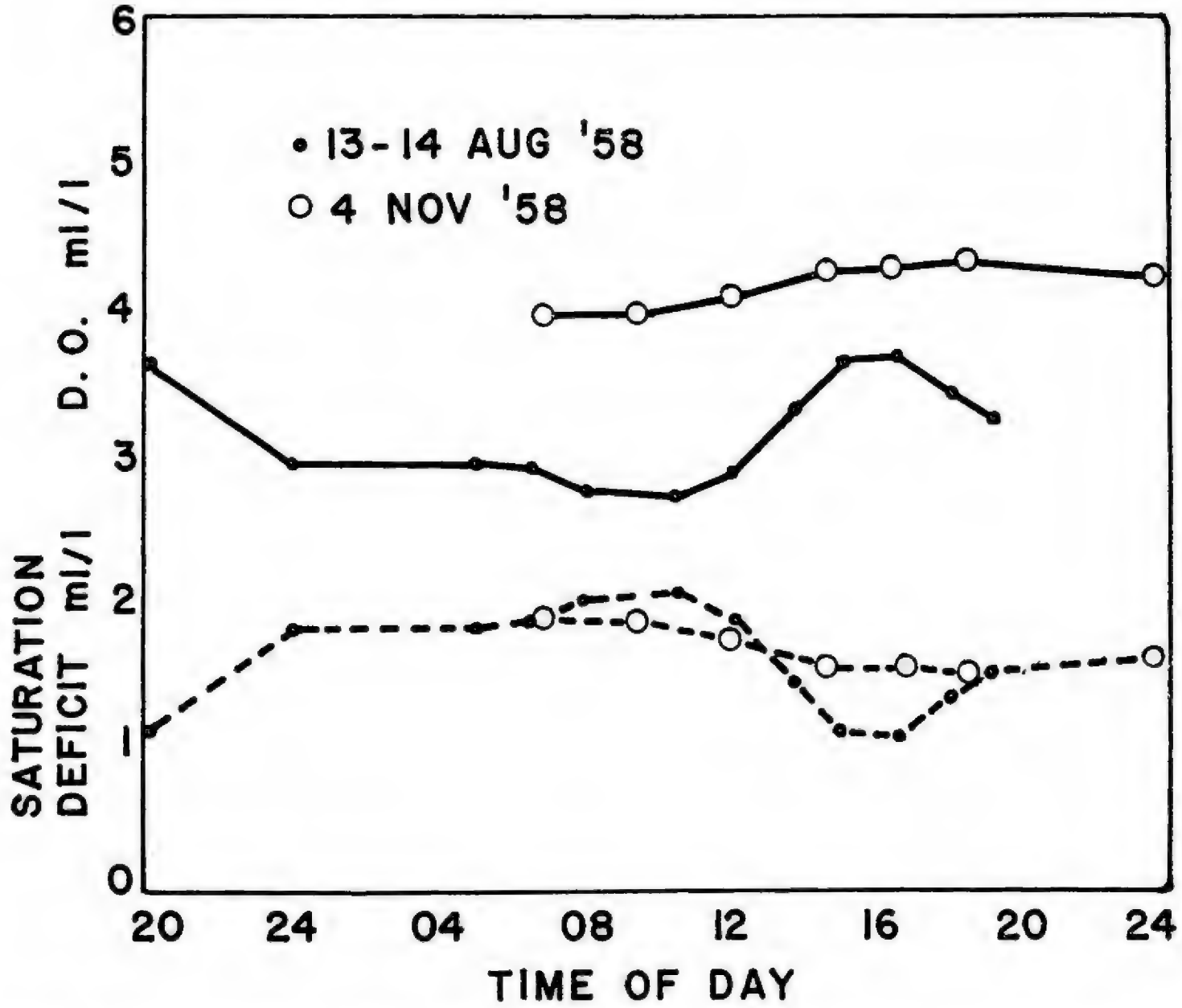

Fig. 6. Diurnal oxygen curves for the Duplin River. Open circles, Nov. 4, 1958; solid circles, Aug. 13–14, 1958.

Dinoflagellate blooms which occur nearly every spring in the region upstream from the Forks station are necessarily always autotrophic in character regardless of temperature.

Light

The limiting effect of light on photosynthesis of natural phytoplankton populations has been investigated by Edmondson (1956) and Verduin (1954) for lakes and by Jenkin (1937), Sverdrup (1953), Ryther (1956b), and Steeman-Nielsen and Hansen (1959) for the sea. Sverdrup (1953) analyzes the effect of light in terms of the compensation depth of the plankton community. He points out that for a given compensation depth the mixing layer cannot exceed a certain depth without reducing the net productivity in the water column to a negative value since the portion of the time that the algal cells are exposed to the light depends on these two depths. The critical depth (D_{cr}) is the depth of the mixing layer for which photosynthesis and respiration are exactly balanced, that is net production equals zero. The critical depth in turn is a function of the extinction coefficient and the ratio of the radiation passing the sea surface to that reaching the compensation depth.

Sverdrup's solution of this relationship is:

$$\frac{D_{cr}}{1-e\exp-kD_{cr}} = \frac{1}{k}\frac{\bar{I}_e}{\bar{I}_c} \tag{1}$$

where $\bar{I}_e$ = amount of radiation passing the sea surface,
$\bar{I}_c$ = amount of radiation reaching the compensation depth, and
k = extinction coefficient.

Since the denominator of the left hand term of the equation approaches one for values that would ordinarily be encountered, a close approximation and a more useful form of the expression is:

$$D_{cr} = \frac{1}{k}\frac{\bar{I}_e}{\bar{I}_c} \tag{2}$$

Substituting

$$\bar{I}_c = \bar{I}_e\, e\exp-kD_c \tag{3}$$

$$D_{cr} = \frac{e\exp+kD_c}{k} \tag{4}$$

where D_c = compensation depth,

thus demonstrating that the critical depth depends ultimately on the compensation depth and the extinction coefficient. When D_{cr} exceeds the thickness of the mixing layer, an increase in the phytoplankton population is possible, but when D_{cr} is less than the thickness of the mixing layer, no increase is possible.

In tidal rivers and sounds adjacent to Sapelo Island, mixing is complete, and the mean depth of the area can be taken as the thickness of the mixing layer. Making this substitution and using the mean extinction coefficients where available the D_{cr} values for the light and dark bottle experiments were calculated. These D_{cr} values (Tables 1, 2, and 3) are estimates since compensation depths for the bottles represent compensation depths

for the plankton community, not for the phytoplankton alone. Net production was observed only when D_{cr} exceeded the mean depth, while no net production was observed when D_{cr} was less than the mean depth. In seven cases when D_{cr} exceeded the mean depth, bottle net production was negative. These cases do not constitute exceptions, since the condition that D_{cr} exceed mean depth is necessary but not sufficient for net production of phytoplankton and since the possibility of net plant reproduction is not ruled out by negative data on net bottle production. Other factors, such as grazing or the intrinsic condition of the phytoplankton population may also prevent a net increase of the phytoplankton.

Because the methods measure different quantities, these results cannot be compared directly with those of Thomas *et al.* (1957) for the Mississippi Delta waters. The oxygen evolution method as used here estimates gross primary production minus community respiration, while the C^{14} method used by Thomas *et al.* may give an estimate of net phytoplankton production uncorrected for bacterial respiration.

Blooms

It is significant that dinoflagellate blooms have been observed repeatedly (usually every spring) in the region upstream from the Forks station and also in other shallow tidal creeks (Pomeroy *et al.*, 1956); (Ragotzkie and Pomeroy, 1957), while there have been no blooms observed below this point or anywhere in Doboy Sound. Oxygen data show that these blooms develop with a high net production rate. Thus, the limitation on net production in local waters imposed by light may be severe enough wherever the average depth is greater than three or four meters to effectively prevent the development of blooms.

Annual Net Production

The mean net annual production of the plankton community including organic detritus and its associated bacterial flora at the lower and upper ends of the Duplin River was -0.038 and -0.16 gm C/m^2/day respectively. Since the metabolic activities of all other animals in the estuary would tend to increase the net loss of organic matter from the system, an outside source of organic matter is necessary to account for the negative production. The most likely source is the salt marsh which covers about three-fourths of the total area between the mainland and the ocean beaches (Figure 1). The net production rate of the marsh grass (primarily *Spartina alterniflora* Loisel) is estimated to be on the order of 1 gm C/m^2/day (Smalley, 1959), an order of magnitude higher than the loss cited above.

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Measurements of Productivity of Turtle Grass Flats, Reefs, and the Bahia Fosforescente of Southern Puerto Rico[1]

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Abstract

Measurements of oxygen, gross production and community respiration were made in two seasons and in 15 environments of southern Puerto Rico including coral reefs, sheets of anemones, turtle grass, and a luminescent bay. Metabolism ranged from 1 to 44 gm oxygen/m^2/day. Production and respiration were greatest on the coral and anemone reefs and least in the phosphorescent bay. Seasonal changes were relatively small. New ways are given for analyzing diurnal curves of oxygen to obtain estimates of community metabolism.

Introduction

Among the tropical environs of the sea the reefs, grass flats, and mangrove-lined estuaries are the most productive of all natural ecological systems. High values of both total community respiration and gross photosynthesis have been reported in the range from 10 to 35 dry gm organic matter/m^2/day (reefs: Kohn and Helfrich, 1957; grass flats: Odum, 1957). Such conversion of the sun's energy is as great as in maximum sustained agriculture and algal culture (Odum and Odum, 1959).

However, data from tropical environments are few and inadequate for generalization. For example, it is not known if photosynthesis is generally greater where plants are mainly of symbiotic type and located within animals as in animal reefs or where free living plants are dominant as in grass flats. The true mutualistic exchange of nutrients and organic matter in a symbiotic association has been shown recently by Muscatine and Hand (1959). Goreau (1960) questioned that there was a large magnitude of or-

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FIG. 1. Aerial photograph of reefs, grass flats, principal islands and the edge of the Bahia Fosforescente on the southwest coast of Puerto Rico west of Lajas. The aerial photograph was furnished by the Commonwealth of Puerto Rico. Some principal locations referred to in this paper are indicated on the face of the figure.

ganic carbon transfer. However, his experimental light intensities were much less than those reaching surface corals. Any experiment designated to test magnitudes of net production must be made in full light. Additional data from nature are needed.

In the vicinity of La Parguera and the Instituto de Biologia Marina (Zoological Garden) on the south shore of Puerto Rico are a series of distinctive reefs, grass flats, and bays. See aerial photograph in Figure 1. Blue Caribbean water flows gently over and among the small reefs and islands under predominantly sunny skies, for this shore is in the dry region of the island rain shadow. The land vegetation is arid, but the fringes of the land are lush with mangroves. The turtle grass beds and coral reefs are interspersed, and mixed coral and grass also occurs. In many areas white calcareous muds typical of tropical banks comprise the substratum. Unlike the reefs that dominate parts of Eniwetok, there are very extensive continuous sheets of live coral and anemones. Over large areas the only plants are within the coral tissues or in shaded crevices among the corals. Similarly some sheets of anemones are in a nearly continuous carpet. The chlorophyll per area (0.5 to 2.0 gm/m^2; Odum, McConnell, and Abbott, 1959) in these environments is as great as in many terrestrial environments and greater than in most aquatic communities.

Among the peculiar environments in the vicinity of the institute is Bahia Fosforescente, a mangrove-bordered bay (Figure 2) widely known for its intense luminescence (Margalef, 1957; Coker and Gonzalez, unpublished manuscript; Burkholder and Burkholder, 1958).

In this paper are reported some field measurements of oxygen made day and night in various water flows near La Parguera. Several kinds of reasoning are used to convert the observed changes in oxygen content into estimates of the metabolism of the communities. In several of the series reported, incomplete measurements of the flux of water may limit the accuracy of the interpretations, but there can be no question of the tremendous metabolic activity of these tropical marine complexes. Natural systems, in maximal development, are as metabolic as are man's cultivated systems of algal culture and agriculture.

ACKNOWLEDGMENT

We are grateful to Dr. R. E. Coker for stimulating our interest in these areas and to Ronald Wilson for help with the day and night sampling. Daniel and Pedro Rosado at the Institute of Marine Biology faithfully took the authors to the reefs at all hours of day and night.

Methods

Oxygen determinations were made with the Winkler method. Current flows were estimated with dye and watch. In some determinations, current was not measured as often as oxygen. Therefore, estimates of metabolism, calculated at times when current was not measured, are only approximate. Several kinds of oxygen series were obtained and analyzed as follows:

1. *Upstream-downstream change method.* Oxygen was measured upstream and downstream with respect to the current on a measured segment of reef or grass flat. The changes were computed per volume of water and converted to estimates per areas as previously described (Odum, 1956; Odum and Hoskin, 1958). The procedure involves construction of an oxygen rate of change graph as does the next method. An example of

the daily photosynthesis-respiration cycle determined by the upstream-downstream method is shown in Figure 3.

2. *Method of measuring changes within a water mass.* Where water was moving about in the same area, measurements from several simultaneous samples were averaged to obtain an oxygen value representative of the water mass. A rate of change curve was computed from the single oxygen curve; an aeration constant was computed and used to correct the curve; and metabolism was computed as indicated previously (Odum and Hoskin, 1958). The aeration constant found over the reefs was about 1.0 gm $O_2/m^2/hr.$ at zero per cent saturation. In deeper waters over the grass flats, where turbulence was less, aeration constants were about 0.4 $gm/m^2/hr.$ at zero per cent saturation. An example of the photosynthesis-respiration cycle determined by the method of measurements within a water mass is shown in Figure 4.

3. *Method of minimal computation for steady states with uncertain advective admixture from less productive areas.* When water is moving over productive environments that are similar, the oxygen may simultaneously rise and fall during day and night over a large area. Computations may be made as in Method 2. If there is some advection of water from nearby zones where there is not much daily oxygen change, and if this ad-

FIG. 2. Aerial photograph of the Bahia Fosforescente. The bay is about 0.85 mile in width. The white arrow indicates the station where dark and light bottles were filled and suspended. Picture was taken Dec. 31, 1950. Number Gs-LR-6 191, Commonwealth of Puerto Rico.

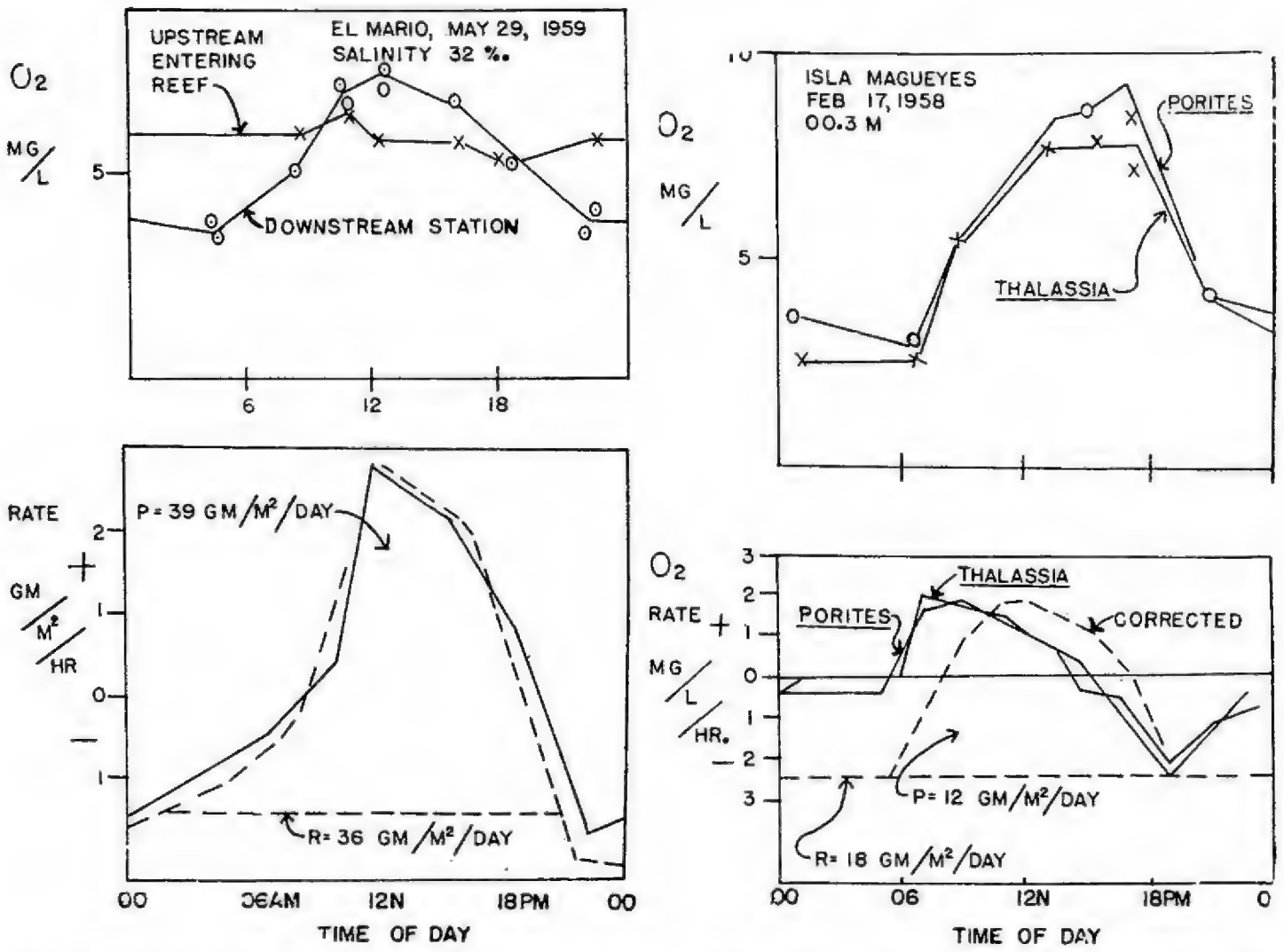

FIG. 3. Oxygen data from El Mario Reefs, May 29, 1959. Oxygen values from deep incoming water and after passage over *Millepora*, *Zoanthus*, and soft coral bottoms are given in the upper graph. The rate of change in the water in passing across the reef is calculated in the lower graph. These data are representative of the upstream-downstream type calculations, where advection between the two stations is not large.

FIG. 4. Oxygen data from the southern shore of Isla Magueyes, Feb. 17, 1958. Oxygen data are reported in the upper graph for two stations. In the lower graph the rate of change is computed from the upper graph on the assumption that there is a single homogeneous water mass and bottom. Such computation provides a minimal estimate since any advection from the deeper waters tends to diminish the range between peaks and valleys of the graph.

mixture is undetected, the calculations will provide under-estimates of the metabolism. This is because the mixing of water from areas of less diurnal oxygen amplitude will tend to lower the range of oxygen in the samples and thus lower the estimate of metabolism below the correct value. The times of maxima and minima may not be disturbed.

For example, suppose that some blue water with little diurnal oxygen variation from deeper water is mixing in with water flowing over the reef. The peaks in the oxygen curve over the reef will be diminished and the diurnal curve calculation will be minimal. In several situations in this paper such calculations are reported and their minimal nature indicated by a plus (+) sign.

For example, on March 13–14, 1958, a strong diurnal curve was obtained at a single station over a grass bed on the margins of the Bahia Fosforescente (Figure 5). Consider the grass metabolism by calculations first with one assumption concerning water flow and then with an opposite assumption.

A. Suppose that the water has been moving across beds of equal productivity so that one may treat the curve as representative of one water mass. Diurnal curve analysis (Method 2) yields P and R about 6 gm/m²/day.

B. In contrast, suppose that the water has been moving directly from the open water,

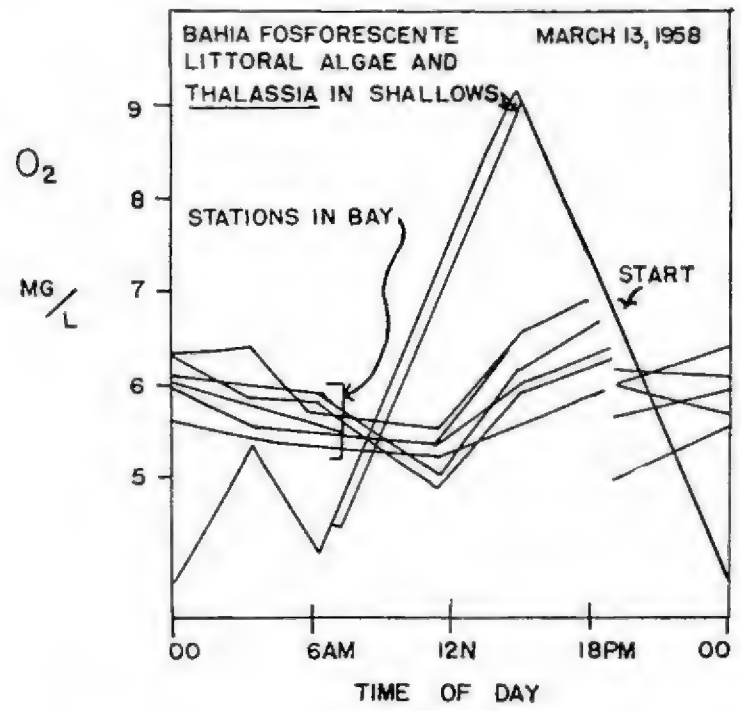

FIG. 5. Oxygen data from seven stations in the Bahia Fosforescente, March 13–14, 1958. A composite average was used to compute a rough approximate metabolism for the entire bay by shifting the time scale six hours. The estimate is likely to be minimal since the lag in water movement from shallows to the middle tends to diminish the peaks which would occur if the plankton oxygen production and advective lateral mixing from oxygen production in the shallows were contributing to the observed water oxygen content at the same time of day. The production of the *Thalassia*-algal bed was computed separately.

of fairly constant oxygen concentration, to the grass flat with an average speed over the grass of 1.5 m/min. (an observed current at one time of day). By this assumption one is calculating large oxygen changes for a short period of time. Values of P and R are about 48 gm/m^2/day.

It is likely that the correct answer is in between, for neither assumption is correct. The water has been drifting over the grass neither for as long as in A nor as short a time as in B.

Thus, one can make some bounding estimates even when adequate water movement data are not available.

4. *Method of computation with uncertain advective mixture from a more productive area; computation including metabolism of both areas which are intermixing.* When water flows from a more productive area into an area of less metabolism, in which measurements are being made, delayed peaks are produced and the amplitude of oxygen change is greater in the measurement area than would have been the case without the mixing. Diurnal measurements from such curves thus include both the metabolism in the measurement area plus the large changes due to advection. Such cases involving mixing from productive zones are easily recognized by the delayed times of maxima and minima.

The curves for the Bahia Fosforescente in Figure 5 are an example. The tremendous production in the grass flat shallows is indicated by the diurnal curves there. Peaks on the grass flats occur at expected times of day. In the inside of the round bay, however, maximum oxygen arrives six hours late after the sun is down and minimum oxygen arrives six hours late after the sun is up.

To make an approximate computation of the bay as a whole including all stations, one may displace the peaks in time six hours. The curve, thus analyzed for metabolism, yields a value 8 gm/m^2/day. Such computations are minimal since the small rise and

fall of oxygen due to metabolism in the open bay tends to come at a different time from the mixing of high or low oxygen water from the shallows, and the two effects cancel. Even so, the best estimate of the overall metabolism of the Bahia is obtained from such curves, which were similar for three different days. The role of the grass flats in the overall nutrition of the bay is clearly indicated. Advection of oxygen may also be accompanied by net advection of organic matter.

As described elsewhere (Odum and Hoskin, 1958), the diffusion exchange with the atmosphere can be measured from the daily curve itself where adequate night data exist. Work with shallow, marine, flowing environments has established the order of magnitude of diffusion for a given saturation gradient of about 1 gm/m^2/hr. for 100 per cent saturation deficit (Kohn and Helfrich, 1957; Odum and Hoskin, 1958). In several instances in this paper where night data were incomplete, the observed metabolism has been obtained by correcting for diffusion using the above value for the diffusion constant.

Measurements of the Reefs and Grass Flats

A summary of the measurements of production and respiration from a number of varied environments are given in Table 1. Examples of the kinds of oxygen data used are provided in Figures 3 and 4 (El Mario, Feb. 22–23, 1958 and southern shore Isla Magueyes, Feb. 17, 1958). In general, oxygen is maximal in late afternoon and minimal at dawn.

There is no question about the tremendous metabolism. The measurements (11–44 gm/m^2/day) completely confirm previous high estimates. Even solid sheets of coral (*Porites*) or anemones (*Zoanthus*) exhibit enormous photosynthesis. There was excess production by the coral reefs in some curves whereas in others respiratory metabolism as estimated from the night oxygen change exceeded photosynthesis over a 24 hour period. The coral association quantitatively produces more organic matter than it uses. The reefs previously studied at Eniwetok (Odum and Odum, 1955) contained an abundance of filamentous algae in between coral heads, on rubble, in rock substrates, in sand, and in clumps. In several of the Puerto Rican reefs studied, however, continuous sheets of animals exist with plants mainly of symbiotic type. Even in these reefs photosynthesis was as great as respiration.

Metabolism of coral was higher than that of the turtle grass. Factors favoring high photosynthesis on the reef are high current for circulation, shallower conditions permitting more light penetration, and localized symbiotic regeneration of nutrients. Burkholder and Burkholder (1959b) found chlorophyll in all the important reef organisms including anemones and soft corals.

Values for turtle grass (*Thalassia*), 8–15 gm/m^2/day, fall within the range of values found in Texas (Odum and Hoskin, 1958), but unlike the flats in Texas there was little seasonal difference found from January to June. Burkholder and Burkholder (1959a) found 2800 gm dry weight/m^2 of turtle grass including rhizomes.

Bahia Fosforescente

In Figure 5 are oxygen curves for the waters of Bahia Fosforescente. Except for the station over the shallow turtle grass, the curves are of different shape from those over the reefs and flats and different from that in most kinds of environment (Odum and

TABLE 1

Oxygen Metabolism (grams/m²) in the Waters of Southwestern Puerto Rico

(Pcn=net daytime community photosynthesis per hour; R=night time community respiration per hour: Pg=net photosynthesis per day with night R added; R_{24} = 24 hour community respiration based on night R.

Community and location	Depth (m)	Current (m/min)	Temp. (°C)	Date	Time	Method used key below	P_{cn}	R	P_g	R_{24}
East La Gata Reef,				Feb. 27	1310	AF	1.75	.....	.....	.....
Porites reef	0.26	7.6	27.5	1958	1335	AF	2.8	.....	....	.....
La Gata, *Thalassia* bed	.....	7.3	27.5	Feb. 27 1958	1100	AF	2.8	.....	.....	.....
La Gata Reef, *Porites* and *Thalassia*	0.3	slight	25–28	Feb. 18 1958	24 hrs.	BC	1.8+	1.8+	8.6+	11.3+
West La Gata Reef, *Thalassia*	0.26	6.4	27–28	Feb. 28 1958	1100	AF	2.6	.....	.....	.....
Margarita Reef, *Porites* carpet	0.23	0–9	25–28	Feb. 25 1958	24 hrs.	A	1.4	0.5–4	44	.....
Isla Magueyes, southern shore, *Porites* and *Thalassia*	0.3	0–3	25–29	Feb. 17 1958	24 hrs.	BC	0.32+	0.75+	12+	18+
La Media Luna, *Millepora*, 18m; *Acropora* and *Porites* 65m	0.28–3	5–8	28–30	June 12 1959	24 hrs.	AC	2.0	1.21	38.4+	29+
Las Palmas, *Thalassia*	0.3	1.8	25–28	Feb. 28 1958	1237	AF	1.33	.....	.....	.....
Channel north of Isla Magueyes, *Thalassia*	1.2–1.5	4.2	26–28	Feb. 13 1958	24 hrs.	BG	0.50	0.52	10.5	12.5
	1.2–1.5	....	25–28	Mar. 1 1958	24 hrs.	BG	0.60	0.45	11.0	12.5
	1.2–1.5	....	28–29	May 29 1959	24 hrs.	BG	0.60	0.60	14.0	14.5

TABLE 1 (Continued)

Oxygen Metabolism (grams/m²) in the Waters of Southwestern Puerto Rico

P_{en}=net daytime community photosynthesis per hour; R=night time community respiration per hour; Pg=net photosynthesis per day with night R added; R_{24} = 24 hour community respiration based on night R.

Community and location	Depth (m)	Current (m/min)	Temp. (°C)	Date	Time	Method used key below	P_{en}	R	P_g	R_{24}
Enrique Reef, Millepora Thalassia Zoanthus, Dictyota, Porites	0.1–0.6	6.4	27–29	Mar. 12 1958	24 hrs.	A	2.0	0.90	20.0	17.3
El Mario Reef	0.39	4–8		May 29 1959	24 hrs.	AF	1.6	1.5	39	36
Bahia Fosforescente, Total Bay	4	....		Jan. 24 1957	24 hrs.	B	0.08	0.28	5.6	7.7
Plankton only	4	....		Jan. 24 1957	24 hrs.	D (Table 2)	0.06	0.09	1.4	2.3
Thalassia bed	.....	....		Feb. 12 1958	24 hrs.	BC	0.85+	0.75+	15+	18+
Thalassia bed	.....	....		Mar. 13 1958	24 hrs.	BC	.....	.....	5+	6+
Total Bay	4	....		Mar. 13 1958	24 hrs.	See text	.....	.....	<48	<48
						C	.....	.....	8.8	7.7
Plankton only	4	....		June 1 1959	24 hrs.	D	—0.18	0.29	1.4	6.9

A. Upstream-downstream change
B. Diurnal curve—single water mass method
C. Since there is some admixture of water from other areas, this estimate is minimal
D. Dark and light bottles
E. Data over a 24 hour period
F. With standard diffusion correction
G. Upstream-downstream measurements were similar and averaged.

Hoskin, 1958). Maximum oxygen occurs just after sunset and minimum oxygen occurs just before noon. The following interpretation is offered.

If waters are circulating and exchanging from a very productive nearby bottom community into a measurement area in which metabolism is low, the high oxygen values following the day's activity in the productive zone will move into the measurement area several hours later. Similarly, the low oxygen values of high respiratory metabolism achieved by the nighttime consumption will move from the productive zone into the measurement area several hours late. In the Bahia Fosforescente the shallow grass flats and reefs at the entrance and margins (Figure 2) may provide advective lateral mixing with sufficient daily oxygen range to produce a delayed peak in the central deeper bay. Thus, the middle of the bay continues to increase in oxygen content for several hours after the maximum *in situ* photosynthesis has been attained. Similarly, oxygen continues to diminish after sunrise as waters with low oxygen are mixing into the open bay from the shallows. The marginal plants are listed by Almodovar and Blomquist (1959).

Some additional evidence that the deeper central bay area of the Bahia Fosforescente is not productive can be obtained from the bottle experiments described below which indicate a minor role of the plankton.

Some estimate of the whole metabolism of the bay may be had by averaging the separate data of the several stations in the bay and treating the combined curve as a single mass. The results in Table 1 indicate the important role of the shallows and the relatively lower productivity of the bay in comparison to reefs and flats.

In some of the diurnal curves and bottle series in the Bahia, respiration is greater than photosynthesis suggesting a net import of organic matter such as may be provided by the mangrove swamp waters observed to bring tan substances into the Bahia from the margins.

Photosynthesis and Luminescence

The plankton in the bay have been studied by Margalef (1957) and Coker and Gonzalez (1960). The brilliant luminescence is produced by dinoflagellate populations. Boat wakes, hundreds of yards distant, appear silvery-white even in full moonlight. When chemicals are added to oxygen samples in the Winkler process there is a momentary flood of light as from an electric flash bulb. No luminescence observed by the authors at Woods Hole, Massachusetts; Alligator Harbor, Florida; or in the Laguna Madre of Texas has been so bright. Although not measurable with ordinary photometers, Dr. George Clarke of Woods Hole Oceanographic Institution has recently measured the light emission with photo-multiplier apparatus (Clarke and Breslau, 1960). The question can be raised as to the amount of photosynthesis taking place in water with a bright development of dinoflagellate luminescence. Since the luminescence is from dinoflagellates it might be inferred that a bright luminescence was a result of unusual abundance of dinoflagellates and a state of high productivity. Some dark and light bottle experiments were made to measure the plankton metabolism in the luminescent water (Table 1).

An example of 24-hour measurements of oxygen change in dark and light bottles suspended in the bay is reported in Table 2. In the first measurement on January 24, 1957 the bottles were filled with water from the top during the day. In the second bottle series in June, 1959, the bottles were filled from a carboy that was filled from the lower levels after sunset. The similar results from both series as well as the even distribution of luminescence suggest that the dinoflagellates were present in the bottles in representative

TABLE 2

Twenty-four hour dark and light bottle measurements in the Bahia Fosforescente January 24, 1957, at a depth of four meters

	Oxygen in bottles in mg/l			
Data	Replications			Mean
Start	5.78	6.25	6.32	6.11
Dark	5.80	5.47	5.38	5.53
Light at				
1.5 m	5.73	5.67	5.82	5.73
2.5 m	6.24	5.98	5.68	6.13
3.5 m	5.82	5.68	5.85	5.78

Calculations	Metabolism in gm/m²/day
R Respiration: (6.11–5.53) (4m)	+2.32
P_n Net bottle photosynthesis in 24 hours: (mean of 3 levels—6.11) (4m)	—0.92
P_g Gross photosynthesis R + P_n	+1.40

numbers. The metabolism is relatively small for a bay area. Similarly, the chlorophyll extracted on a millipore filter was only 0.033 gm/m² of bay area, a small value. The metabolism and chlorophyll values were consistent since the ratio of the two (assimilation ratio, 4.3 gm/gm/hr.) was similar to that in other plankton systems (Odum, McConnell, and Abbott, 1958).

Under bottle conditions the respiration exceeded photosynthesis. It may be considered that a population sufficient for bright luminescence need not be accompanied by a large metabolism. The contribution of the plankton is comparatively small compared to the role of the sides and bottoms as indicated by the free water computation. The swampy mangrove margins on one side were observed to release colored, organic-containing waters into the bay. The excess of respiration over photosynthesis is consistent with a situation where organic matter is being imported. An abundant supply of vitamin B-12 in the bay is described by Burkholder and Burkholder (1958).

Summary

1. Measurements of oxygen, gross production, and community respiration were made in 15 environments of southern Puerto Rico during winter and spring of 1958 and early summer, 1959. These included the waters of the shallow coastal shelf, coral reefs, anemone sheets, turtle grass flats, reefs with grass and coral, and a luminescent bay.

2. High rates of metabolism were found ranging from 1 to 44 gm oxygen/m²/day. Photosynthesis by plants in symbiosis with animals on reefs is one of the most efficient of productive environments. There was a fairly close balance of P and R in most curves.

3. Community respiration rates generally exceeded photosynthetic rates in the Bahia Fosforescente, which receives mangrove swamp water, but photosynthetic rates were equal or greater than total respiratory rates in some grass flats and reefs. Reef metabolism exceeded grass metabolism. Deeper waters were less productive and had less consumption than shallow environments. Bottom metabolism was greater than plankton metabolism measured in bottles.

4. Seasonal changes in metabolism were relatively small.

5. Two new viewpoints on analyzing diurnal curves are suggested for situations where flow data are incomplete: (a) use of diurnal curve as a minimal estimate where sur-

rounding waters are less metabolic; (b) recognition of time lag in maxima and minima indicating advection from areas of greater metabolism.

6. Brilliant luminecence in dinoflagellate plankton populations does not require a large concurrent photosynthesis.

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NOTE ADDED IN PRESS. In an experiment on El Mario reef, June 6, four *Porites* heads were placed in bottles at 0.3 m depth at 10 a.m. After exactly 24 hours under conditions of natural light, all bottles were found to have increased in dissolved oxygen. Thus photosynthesis exceeded respiration in these single heads.

Mobility of Partially Submersed Shells

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Abstract

Some 350 flume tests were conducted with shells of pelecypods, *Dinocardium robustum* Solander and *Anadara braziliana* Lamarck, to determine how physical characteristics of shells affect their ease of movement when partially submerged in swash water on a beach. The distance moved by a shell in the flume varied inversely with the square root of the effective density. The force required to move the shells was directly proportional to the normal component of the weight. Air entrapped beneath shells decreased the normal component of the shell weight so that they could be moved by a smaller force. Shells with holes bored in them did not entrap air and traveled relatively small distances in the flume.

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Introduction

Shells are commonly used by the paleoecologist to reconstruct ancient environments. Before basic conclusions can be inferred from shell distribution, however, it is necessary to determine whether shells are indigenous or exotic, and to estimate the degree of sorting. Basic information concerning factors affecting shell transport may be obtained by studying shell movement in controlled flume experiments.

Menard and Boucot (1951) studied the current velocities necessary to move terebratuloid brachiopod shells in a laboratory flume and found the movement of shells to be primarily controlled by the relative ease of movement of the sub-adjacent bed material. Shape, size, effective density, and ornamentation were also found to influence the velocity required to move a shell. Johnson (1957) performed flume experiments which indicated that current-scouring induced by the presence of clam shells resting on a movable substrate is an effective mechanism for their burial.

The previously mentioned experiments were concerned with the movement of shells completely submerged. The present authors became interested in factors controlling the movement of shells after their initial deposition on a beach. Deposition of a shell on a beach usually does not end its exposure to further transport by water because succeeding swashes and higher tides continue to move the shell. Johnson (1957) conducted experiments in which single valves of pelecypods were set out on a muddy-sand beach just above the low tide mark. When the area was revisited at the following low tide, Johnson found that 40 per cent of the shells had been moved from their original site by currents. Nearly 90 per cent of the shells moved had been those that had originally been placed with the concave side up. Many of the shells which had been placed with the concave side down had been partially or almost completely buried in the muddy-sand. Martin-Kaye (1951) and Lever (1958) have investigated the interesting phenomenon that one valve of a pelecypod is sometimes much more common on a beach than the other. Shells with the concave side down have water beneath when submerged but have air beneath when exposed on a beach (Figure 1). In preliminary flume experiments it was observed that the air beneath a shell tended to make it more buoyant and to increase the ease by which it was moved by water currents. This effect of air entrapped beneath a clam shell on its further transport on a beach has not, so far as the authors know, been previously reported in the literature. The experiments reported in this paper were undertaken in order to determine the manner in which physical characteristics of shells affect buoyancy and the ease of shell movement by currents.

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Shell Buoyancy

One of the oldest physical principles is that of Archimedes, which states that the buoyant force on immersed bodies is equal to the weight of displaced liquid. This princi-

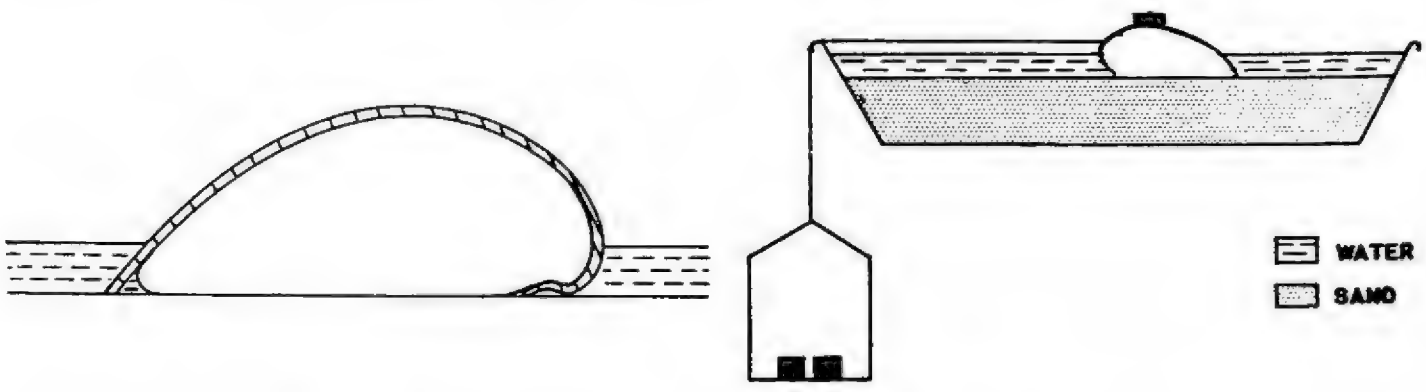

FIG. 1. Position of shell partially submerged, concave side down.

FIG. 2. Experimental arrangement used for determining the horizontal force required to move shells partially submerged in water.

ple has important application to the present study of shell movement in the beach environment. When a disarticulated clam shell is deposited on a beach with the concave side down, the concavity fills with air after water drains from around and under the shell. If the shell is again exposed to swash water, it is not only buoyed up by the water displaced by the shell, but also by water displaced by the air entrapped beneath the shell.

The buoyancy of the air in a shell partially submerged (as in Figure 1) may be determined with the following procedure. A shell is first weighed in air (A) and then when partially immersed in water (B). Weighings in water may be made by placing valve concave side down on a balance pan suspended in water. The shell is then turned concave side up and partially filled with water to the same water line previously reached by water during the shell weighing. The additional volume of water required to completely fill the shell is now measured using a burette. This volume of water is converted to grams (C). A hole is drilled through the shell and the shell reweighed in air (A_d) and then reweighed when immersed in water (B_d) to the same water line as before. With the drilled hole in the shell no air is entrapped. The difference between the weight of the shell in air (A_d) and in water (B_d) represents the weight of water (D) displaced by the part of shell wall below water ($A_d - B_d = D$). If the air entrapped beneath the shell creates a buoyant force equal to the weight of water displaced, then,

$$A - B - D = C \qquad (1)$$

where A is the weight of shell in air, B is the weight of shell when partially submerged in water with air entrapped, C is the weight of water displaced by entrapped air, and D is the weight of water displaced by the submerged shell wall.

Results of using the above procedure on two shells of *D. robustum* are given in Table 1. The small differences between A − B − D (column 4) and C (column 5) are considered to be within the accuracy of the method.

Although a shell out of water weighs more than when it is completely immersed, its weight is least when buoyed by entrapped air. For example, a shell of *D. robustum* which weighed 49.9 gm in air, and 31.7 gm when completely immersed without air entrapped, weighed only 26.0 gm when partially submersed concave side down in water 7 mm deep.

Forces Required to Move Shells

The force (F) required to move an object over a surface is approximately proportional to the load; or

$$F = fF' \qquad (2)$$

where f is the coefficient of sliding friction, and F′ is the force pressing the sliding body against, and perpendicular to, the sliding surface (Stewart, 1944, p. 131).

TABLE 1

Comparison of amount of water displaced by entrapped air under *Dinocardium robustum* shells determined gravimetrically and volumetrically

A Weight in air gm	B Weight in 7 mm of water without hole gm	D Water displaced by shell wall gm	A-B-D Water displaced by air entrapped gm	C Water displaced by air estimated volumetrically gm
54.2	21.5	1.3	31.4	33.7
73.1	43.0	2.0	28.1	32.4

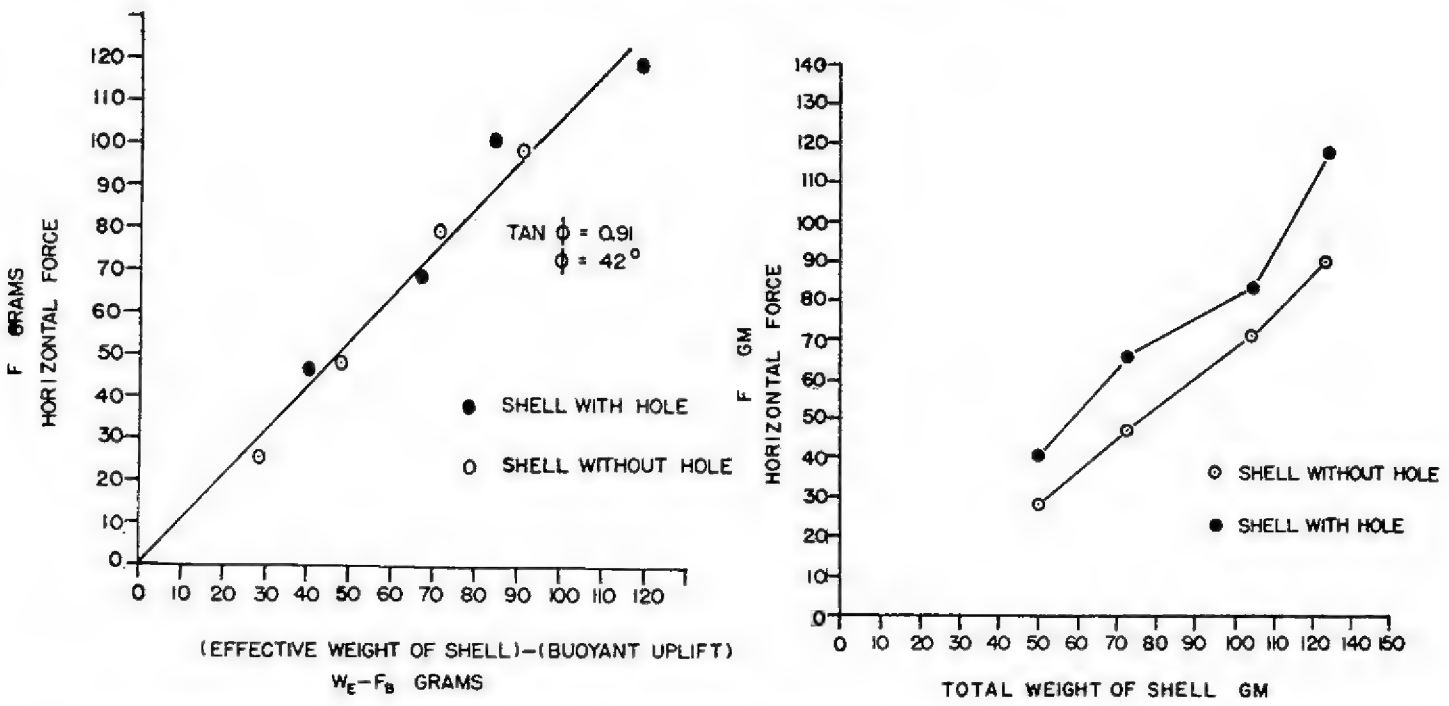

FIG. 3. Horizontal force F required to move a *Dinocardium robustum* valve partially submersed in 0.7 cm of water as a function of the normal component of shell weight ($W_e - F_b$), where W_e is the effective weight and F_b is the buoyant force directed upward caused by entrapped air. The normal weight of the valve was varied by placing brass weights on top of the valve. Data are included from valves with and without holes.

FIG. 4. Horizontal force F required to move a *Dinocardium robustum* valve partially submersed in 0.7 cm of water as a function of the weight of the shell in air. Data and symbols as in Figure 3.

The air under a shell, in addition to the portion of the shell submersed, produces an upward buoyant force so that

$$F' = W_e - F_b \tag{3}$$

where W_e is the effective weight of the partially submersed shell (weight of shell in air less the buoyant uplift due to the water displaced by the portion of shell submerged) and F_b the buoyant uplift due to the water displaced by air. Substituting this in equation (1) then gives

$$F = f\,(W_e - F_b) \tag{4}$$

If a shell should have a hole in the top, there would be no buoyant uplift F_b due to air entrapment, and the corresponding equation would be

$$F = fW_e \tag{5}$$

Thus, theoretical considerations predict that the force required to move a shell when plotted graphically against the quantity ($W_e - F_b$) should fall along a straight line passing through the origin with slope tan (tan $\phi = f$) (see Hubbert and Rubey, 1959, pp. 159–160, for discussion of this principal applied to earth movements). The force required to move a shell with a hole having no buoyancy due to entrapped air when plotted against the quantity W_e should have the same slope as that obtained by plotting force against ($W_e - F_b$), if the coefficient of friction is the same in both cases. Both graphs should pass through the origin and should therefore coincide.

The theory was tested by measuring the force necessary to move shells placed concave down on sand in a pan containing 7 mm of water (Figure 2). Only one shell was used in the experiment in order to eliminate such variables as shape and size. The shell-weight was varied by placing brass weights on the shell. Experiments were first performed with the shell intact and then with a hole drilled through the top and the data plotted in Figure 3. The superposition of the data from these experiments is considered

direct confirmation that the coefficient of friction is the same for the shells with and without entrapped air ($f = 0.91$). The linear relationship in Figure 3 is evidence that the force required to move the shells is directly proportional to the normal component of the weight of the shells.

When the force required to move shells is plotted graphically against the weight of the shells in air (Figure 4), it becomes readily apparent that the buoyancy of the entrapped air allowed the shells to be moved by a smaller force.

Experiments on Shell Transfer in a Flume

Description and Operation of the Flume

Experiments were conducted in a wooden flume having overall dimensions of 41 cm in width and 183 cm in length (Figure 5). An internal flume, or runway, 10 cm wide and 85 cm long was constructed inside the larger flume. The internal flume was necessary in order to obtain desired high velocities with the available water supply. Holes drilled into the exit end of the flume were used to regulate water level. The water level was adjusted by corking certain holes and leaving others open.

Sand from the water's edge one mile south of South Pier on the Mustang Island beach facing the Gulf of Mexico was used in all experiments. The sand is well sorted and typical of beach sand in this area (Figure 6). About 4 per cent of the sand consisted of shell fragments; the balance was quartz sand mixed with a small amount of heavy minerals. During experiments the sand bed was maintained horizontally. A constant bed level was maintained by adjusting the bed and adding new sand before each experiment whenever necessary. The sand layer was approximately 12 cm thick. About one millimeter of scour occurred from around shells during the short duration of each flume experiment. No shells became buried during the trials, but the bed was lowered 10 mm beneath a *D. robustum* valve when the water flow was continued for 20 minutes.

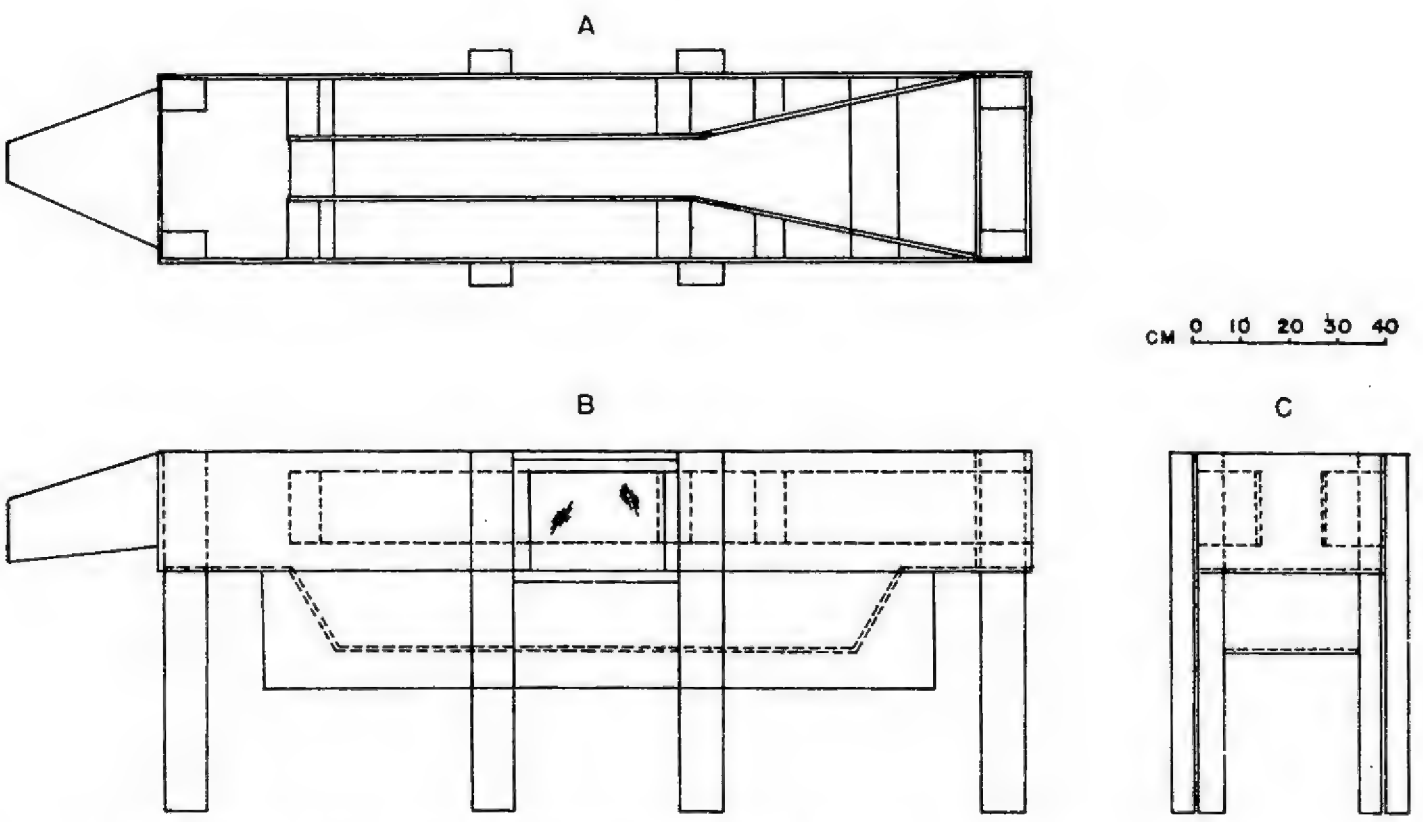

Fig. 5. Diagram of flume used in experiments on shell transfer. A, top view; B, side view; C, end view.

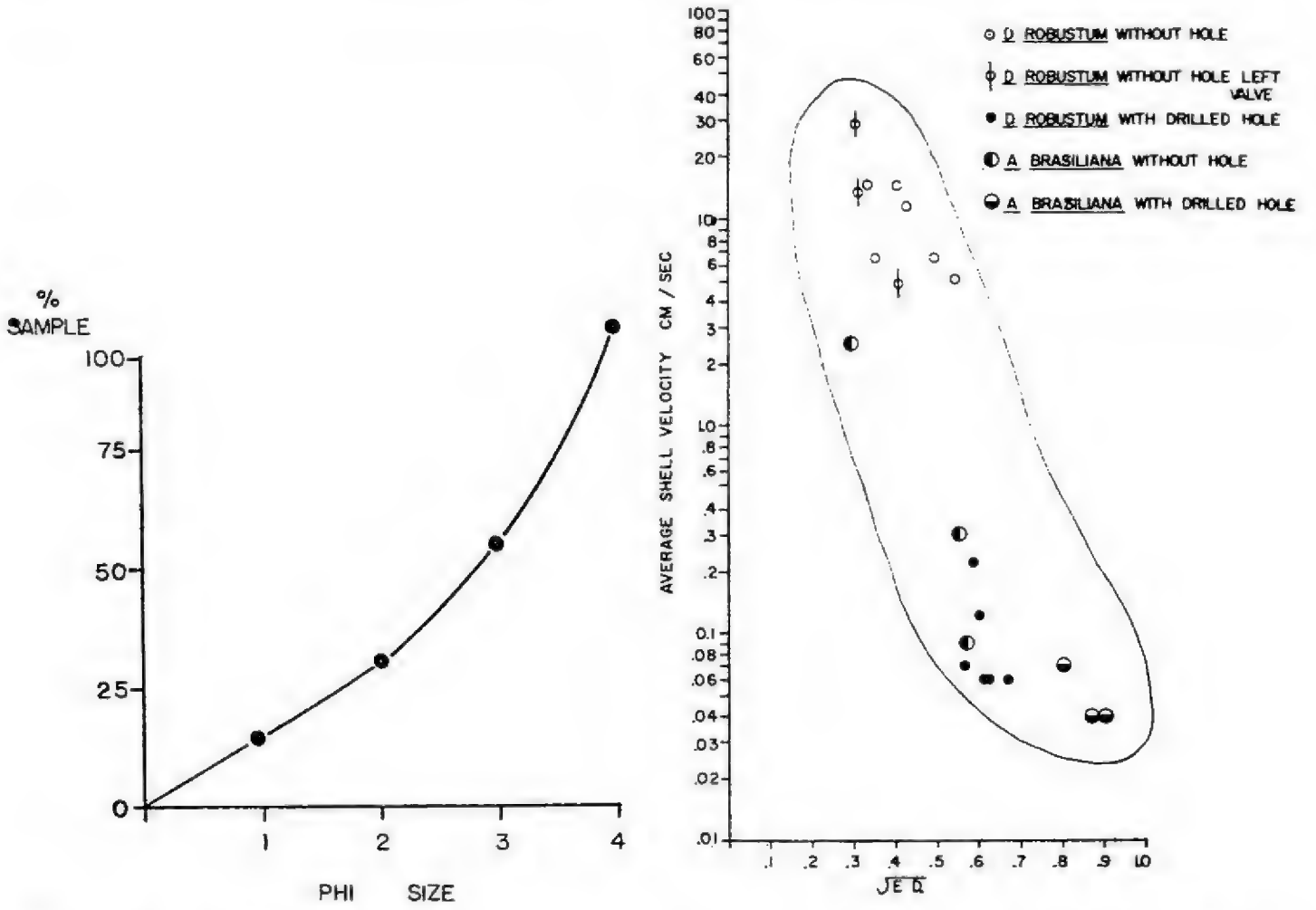

FIG. 6. Size distribution of sand used in flume experiments on shell transfer. Ordinate Phi is — $\log_2$ mean diameter.

FIG. 7. Average shell velocity obtained for each series of flume experiments as a function of the square root of the effective density (ED) of shell upon which the experiment was performed. The effective density was calculated by dividing the weight of the shell when immersed in 0.7 cm of water (W_e) by the volume (V) of the shell. The shell concavity as well as the solid part of the shell is included in the shell volume (V).

Water from a hose was run into a well at the head of the flume. The overflow from the well coursed down the flume and ran out through the holes in the foot of the flume. Water level during the experiments was maintained at 7 mm. Water velocity was held constant at 50 cm/sec. by periodically measuring the rate of discharge and, when necessary, adjusting inflow. The mean current velocity was then calculated by dividing the discharge by the cross-sectional area of flow in the runway. The current velocity was also determined by measuring the velocity of bits of wood placed in the runway. Well water with a salinity of six parts per thousand from Mustang Island was used in the experiments. The air and water temperatures during the experiments were approximately 30° C.

Two pelecypod species were used. *Dinocardium robustum* Solander is a large cockle shell found in abundance washed up on beaches along the Texas coast. Specimens reach three to four inches in size, are oval, inflated, and have many ribs. The species is figured by Abbott (1954, Plate 32, Figure a).

Anadara brasiliana Lamarck is a ribbed ark shell about 1–2½ inches in length. The left valve overlaps the right along the postero-ventral margin. The species is figured by Abbott (1954, Plate 27, Figure y). Ark shells with a shape similar to that of *A. brasiliana* are almost world-wide in occurrence. The family Arcacea extends from the Ordovician to the Recent (Moore, Lalicker, and Fischer, 1952, p. 411).

After the standard condition of water depth and velocity was established in the flume,

a pelecypod valve was placed at a designated place near the head of the flume. All valves used in the experiments were oriented the same way, *i.e.*, convex upward with the beak pointing upstream. The time for the shell to travel 80 cm from the head to the end of the runway was determined with a stopwatch. All experiments were terminated after one minute, and the data reported as distance in centimeters moved by a shell in one minute. The distance traveled by shells which moved more than 80 cm in one minute was estimated by extrapolation. Each series of experiments was repeated a minimum of 10 times. The shells of *A. brasiliana* had a tendency to overturn (15 shells overturned in 110 trials). As hydraulic factors affecting shells in a concave upward position are different than shells in a convex upward position, the velocity data from overturned specimens were excluded in calculating average velocities.

Distances moved by eight specimens of *D. robustum* and three specimens of *A. brasiliana* were measured. These values had air trapped beneath them. Holes were then drilled in each shell and the travel distance in the flume measured. The average distances travelled by the shells are presented in Table 2. Four speciments of *A. brasiliana* with snail-drilled holes were also tested in the flume.

Results and Discussion of Flume Experiments

Flume tests performed by Menard and Boucot (1951) showed that the initial movement of terebratuloid brachiopods depends primarily on the effective density and secondarily on the shape and size of the shell. In the experiments performed by Menard and Boucot, the water velocity required to initiate shell movement was measured. In the present series of experiments, water velocity was held constant (50 cm/sec.) and the distance the shell moved in a given time (1 min.) was measured. The results obtained in each procedure should be related, *i.e.*, if shell A is moved by a smaller current than shell B, shell A will also move farther than shell B when exposed to a current capable of moving one or both shells.

Menard and Boucot (1951) found that initial movement of submerged articulated terebratuloid brachiopods depends primarily on their effective densities. Effective density also seems to be the principal factor affecting transport of partly immersed disarticulated pelecypod values of *D. robustum* and *A. brasiliana;* the distance traveled was related inversely to the square root of the effective density (Figure 7).

Density is defined as the ratio of the mass of a body to its volume. If the body is not of uniform density this definition of density gives an average value. Effective density may be defined by

$$p_e = p - p_w \qquad (6)$$

where p is the mean density of the mass contained in the volume (V) and p_w is the density of water. The volume (V) includes not only shell volume but also volume of the shell cavity in the case of articulated shells (Menard and Boucot, 1951, p. 134). In the present work in which disarticulated shells were studied, the shell concavity was included in total volume when calculating effective density.

The effective density of shells completely covered with water and without entrapped air increases slightly with increase in shell size (Figure 8). This is because the shape of the shell changes little with increase in size, but the shell wall becomes thicker (Figure 9). When the shells of different sizes were partially immersed in 7 mm of water, the effective density of the shells increased relatively rapidly with increase in size (Figure 8). This is because the small shells displaced more water relative to their mass than the

TABLE 2

Physical characteristics and flume behavior of valves

Species and type of valve	Height cm	Length cm	Thickness cm	Weight gm	Sphericity	Normal diameter cm	Hole diameter cm	Cup volume cc	Average wall thickness cm	Weight in 7 mm water gm	Effective density in 7 mm water gm/cc	Average shell velocity cm/sec.	Number of trials
Dinocardium robustum													
Left valve	9.3	8.0	3.4	48.4	0.68	6.4	none	91.2	0.25	13.4	0.12	6.6	25
Left valve	9.3	8.0	3.4	47.0	0.68	6.4	1.3	91.2	0.25	45.1	0.42	.06	15
Left valve	7.2	6.7	2.8	19.1	0.72	5.1	none	46.0	0.20	8.5	0.16	14.3	24
Left valve	7.2	6.7	2.8	18.4	0.72	5.1	2.0	46.0	0.20	18.5	0.36	.12	15
Left valve	6.2	5.8	2.5	12.8	0.73	4.5	none	31.0	0.19	3.7	0.11	14.8	15
Left valve	6.2	5.8	2.5	12.7	0.73	4.5	0.9	31.0	0.19	11.5	0.32	.07	15
Right valve	6.3	8.5	2.6	12.9	0.73	4.6	none	29.0	0.19	3.2	0.10	13.6	10
Left valve	7.3	6.7	2.8	23.3	0.71	5.2	none	46.5	0.22	10.5	0.19	11.6	14
Left valve	7.3	6.7	2.8	23.2	0.71	5.2	0.9	46.5	0.22	20.7	0.38	.06	15
Left valve	7.1	6.8	2.8	25.0	0.72	5.1	none	51.0	0.22	11.0	0.18	11.6	15
Left valve	7.1	6.8	2.8	24.8	0.72	5.1	0.9	51.0	0.22	22.6	0.38	.06	15
Left valve	9.2	8.3	3.5	49.9	0.71	6.4	none	90.0	0.25	26.0	0.24	6.3	15
Left valve	9.2	8.3	3.5	49.8	0.71	6.4	0.9	90.0	0.25	47.1	0.44	.06	15
Right valve	9.4	8.4	3.6	54.2	0.70	6.5	none	105.0	0.25	21.5	0.17	4.8	10
Left valve	9.7	9.2	3.9	73.1	0.72	7.1	none	120.0	0.32	43.0	0.29	5.1	10
Right valve	4.0	3.8	1.6	3.8	0.73	2.9	none	9.0	0.13	0.9	0.09	28.6	10
Right valve	4.0	3.8	1.6	3.8	0.73	2.9	0.5	9.0	0.13	3.6	0.35	.24	10
Anadara brasiliana													
Left valve	4.1	4.0	1.9	12.3	0.77	3.2	none	10.5	0.28	4.4	0.30	0.3	6
Left valve	4.1	4.0	1.9	12.2	0.77	3.2	0.5	10.5	0.28	11.3	0.75	.04	10
Left valve	3.5	3.5	1.5	6.3	0.75	2.6	none	5.0	0.24	2.3	0.32	0.9	8
Left valve	3.5	3.5	1.5	6.2	0.75	2.6	0.5	5.0	0.24	5.9	0.81	.04	10
Left valve	3.6	3.5	1.5	3.2	0.74	2.7	none	3.0	0.20	0.3	0.08	2.5	8
Left valve	3.6	3.5	1.5	3.1	0.74	2.7	0.5	3.0	0.20	2.6	0.64	.07	10
Anadara brasiliana (with snail bored hole)													
Left valve	4.0	4.0	1.7	9.5	0.75	3.0	0.20	9.4	0.25	2.7–8.3	0.21–0.65?	0.4	10
Left valve	2.8	2.7	1.0	2.6	0.71	2.0	0.15	2.8	0.19	1.7	0.14?	13.0	10
Left valve	3.2	3.3	1.4	5.2	0.74	2.4	0.20	5.4	0.23	3.4	0.91?	0.2	10
Left valve	1.7	1.7	0.7	0.6	0.73	1.2	0.12	0.8	0.15	0.2	0.19?	6.0	10

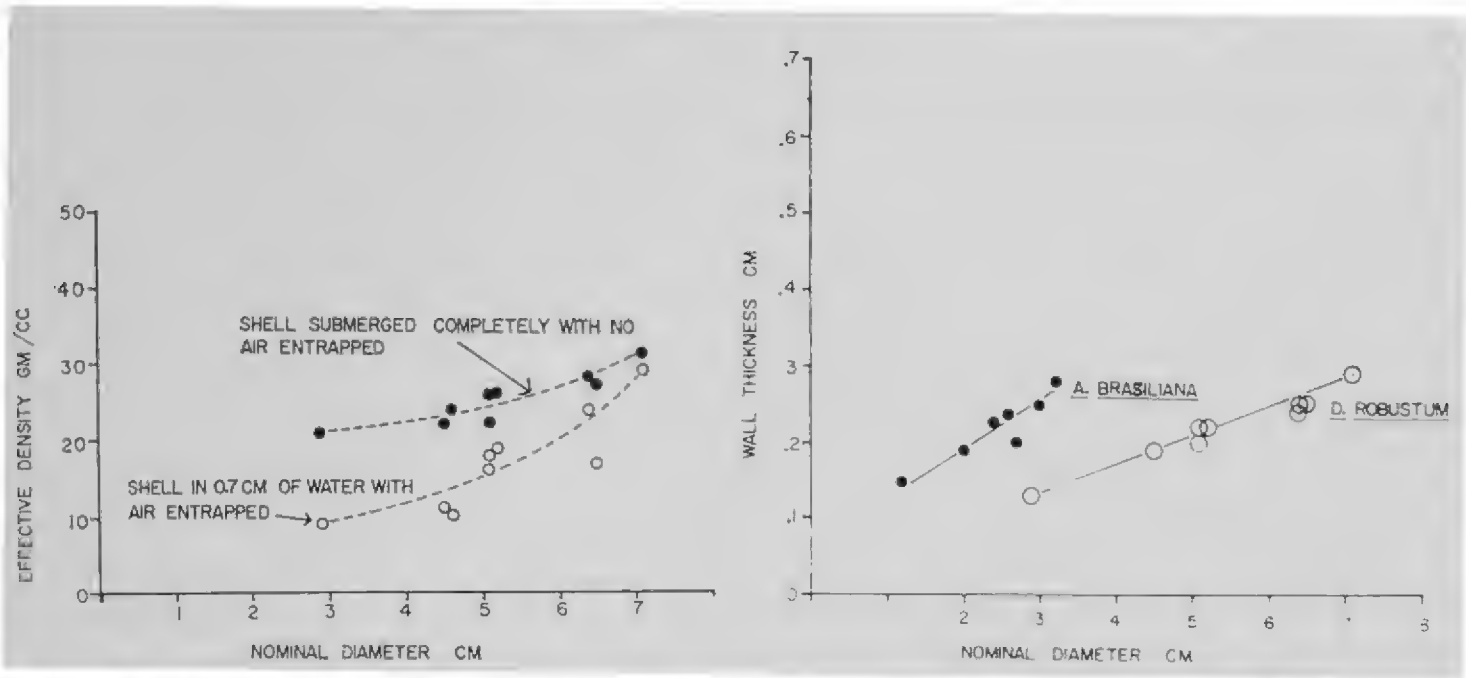

FIG. 8. Effective density of *Dinocardium robustum* valves as a function of the nominal diameter. The nominal diameter is calculated by taking the cube root of the product of the length, width, and thickness of each shell. Shell length was measured along the longest rib in the central portion of the shell. The width was considered the greatest distance between the anterior and posterior margins measured in the plane of commissure and normal to the height. The height is the maximum dimension of the individual valve measured perpendicular to the plane of commissure; height as used here is one-half height of closed articulated shell.

FIG. 9. Wall thickness of shells of *Anadara brasiliana* and *Dinocardium robustum* as a function of nominal diameter. Wall thickness is a term used here to denote the distance between the inner and outer surface of a single valve. Wall thickness was measured with a micrometer at three places along a line parallel to the ventral margin and about one-third the distance from the ventral to dorsal margin; these measurements were averaged.

large shells. If, as indicated in Figure 7, effective density is a major factor in shell transport, and shell size has a greater effect on effective density when shells are only partly immersed, it follows that shells are probably more readily sorted according to size when partially immersed. This suggests that shells are more readily sorted according to size in the beach environment than when completely submerged.

The effect of the air entrapped beneath clam shells in increasing ease of transport becomes very apparent when the distances traveled by shells without air (having a hole bored in shell) are compared with distances traveled by shells of the same size with air entrapped beneath them (Figure 10).

Shells of *A. brasiliana* had higher effective densities than similar sized shells of *D. robustum* because of the thicker shells of the former species (Figure 9). The effect of the higher effective density in decreasing the relative distance transported by *A. brasiliana* is readily seen in Figure 10.

The intercept sphericity (defined by Krumbein, 1941) was calculated for each shell and found to fall between 0.6–0.8. The small differences in the shapes of shells used in the experiments had no measurable effect on shell transport. The simple ornamentation on the species tested had no apparent influence on ease of shell movement.

BEACH EXPERIMENTS

In order to see if the behavior of shells in the flume was representative of their behavior on the beach when exposed to swash water, a series of tests was run on the beach. Two pairs of *D. robustum* shells which had previously been tested in the flume were placed near the water's edge. The left valve of each pair contained a hole drilled through the shell. The valves without holes moved a considerable distance inland with each

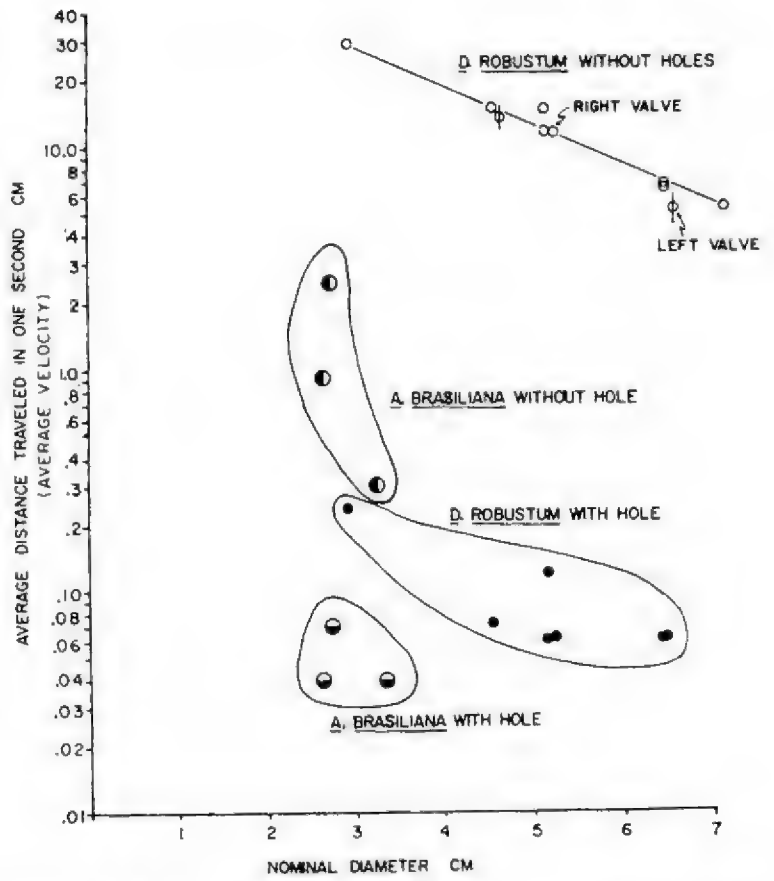

FIG. 10. Average velocity of shells of *Anadara brasiliana* and *Dinocardium robustum* in flume experiments as a function of nominal diameter.

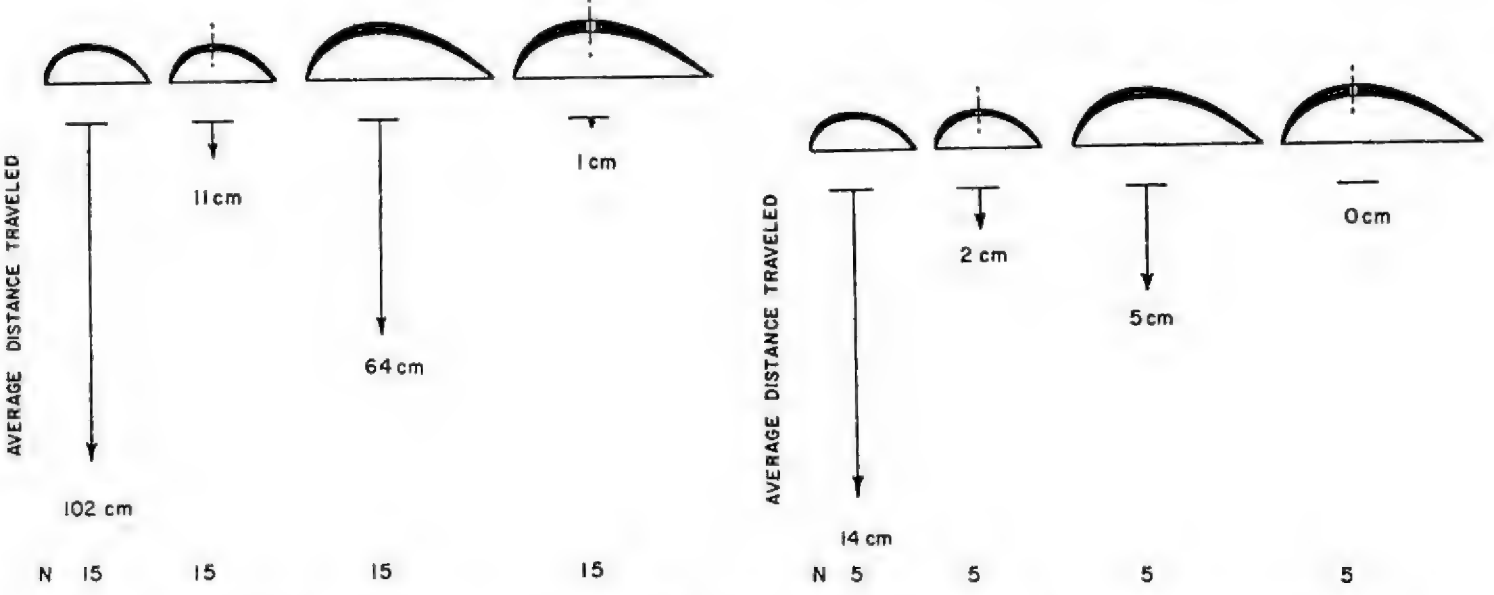

FIG. 11. Distances traveled by *Dinocardium robustum* valves placed at the waters edge and transported shoreward by one, or at most, two swashes. Position of shells and condition of shell (with or without drilled hole) is indicated by shell outlines. Air was entrapped under shells without holes.

FIG. 12. Distances traveled by *Dinocardium robustum* valves placed below low water level during one minute. Same shells as in Figure 10. No air was entrapped beneath valves.

swash, but the valves with holes moved only a short distance, or not at all (Figure 11).

The experiments were repeated in deeper water below the swash area, so that the shells were continuously submerged. Air was allowed to escape completely from beneath the shells before they were placed concave downward on the sand surface. The shells without holes moved farther than the shells with holes (Figure 12). The relatively short distances traveled by the shells without holes were not the result of buoyancy, as was the case with partially submerged shells, but because the hole permitted equalization of the pressure beneath and above the shell, thus deminishing the "lift" due to a decrease in pressure on the upper side caused by the moving water. For discussion of Bernoulli's theorum, which concerns changes of pressure with change of speed, see

Stewart, 1944, p. 181, or standard text on physics. The lifting effect on those valves without holes decreased the normal component of the effective weight of the shell so that it could be moved by slower water currents.

Shell Orientation in Moving Water

Final orientation of a shell which has been exposed to water current reflects current direction. Because of this the process by which shells are oriented is of interest to the paleoecologist. Shells were oriented at the beginning of each flume test with the shell beak pointing upstream. Shells with holes did not move far from where they were placed, and the shells maintained their initial orientation. Shells with air entrapped, on the other hand, traveled considerable distances; these shells were oriented differently at the end of the tests than at the beginning. Left valves rotated counter-clockwise, whereas right valves rotated clockwise. This is opposite the direction of rotation of left and right shells of *Donax vittatus* observed by Lever (1958). The reason for this is that the left valve of *Donax vittatus* more closely resembles in shape and distribution of mass the right valves of *Dinocardium robustum* and *Anadara brasiliana* than it does the left valves. Both in the flume and beach experiments the two species studied became oriented with the posterior end of the shell downstream, and with the beaks of the left valves 90° counter-clockwise from the current direction, and the beaks of the right valves 90° clockwise (Figure 13). The final orientation was probably due, in part, to a tendency of each

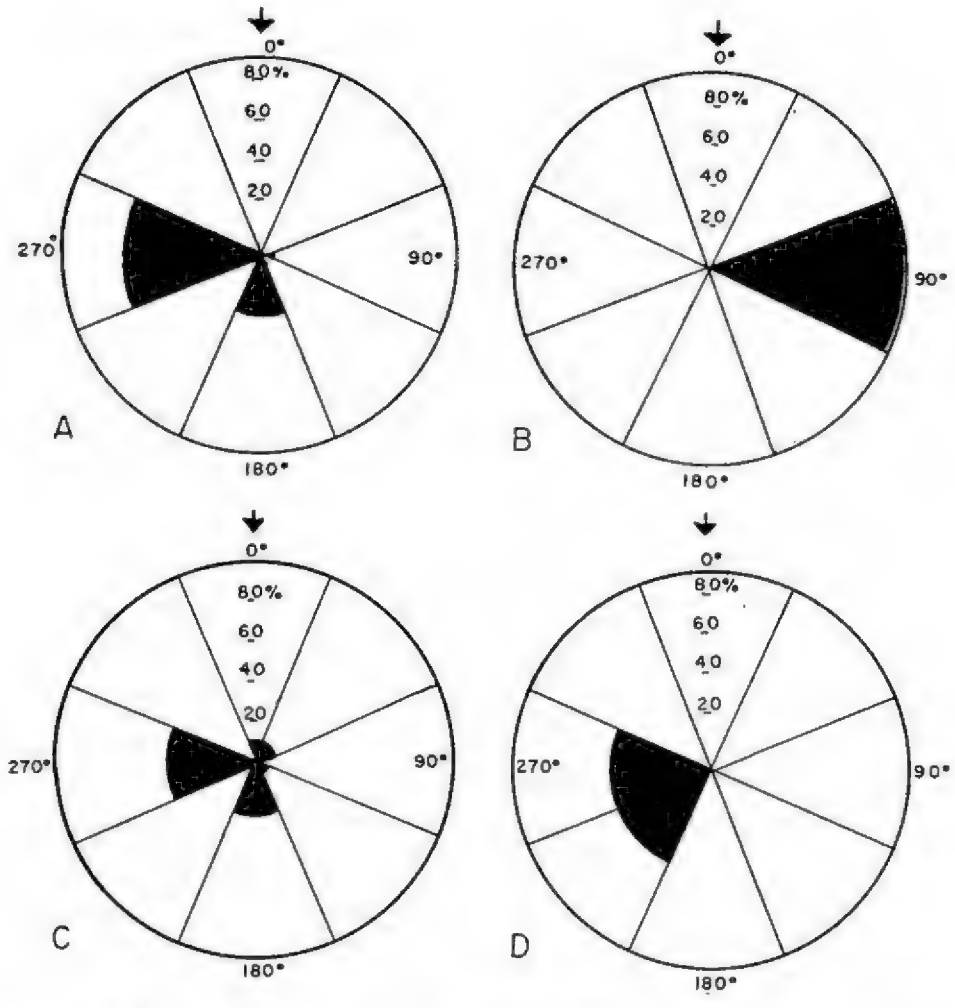

FIG. 13. Orientation of *Dinocardium robustum* valves. Point of reference is the valve beak which in the initial position in A, B, and C, was pointed towards the direction of current source, and in D, was pointed away from source. A, final orientation of right valves in 30 flume experiments. B, final orientation of left valves in 118 flume experiments. C, final orientation of right valves in 20 beach experiments. D, final orientation of right valves in 10 beach experiments. Arrow indicates direction of current.

shell to present its most streamlined silhouette to the current and, in part, to the distribution of mass in the shell. The anterior of the shell, because of its greater thickness, is heavier than the posterior and acts as an anchor while the posterior part trails downstream.

Orientation observations were restricted to shells with air entrapped beneath them. As data are not available showing how these shells become oriented when completely submerged without air entrapped, it is not possible to determine whether the presence of air beneath the shell affected the final orientation. However, air entrapped beneath clamshells probably plays a major part in determining their final orientation. For example, air beneath *D. robustum* valves in a centimeter or more of water tends to lift the umbo of the shell. Observations at the beach showed that when this occurs the umbo of the shell swings towards the beach with a gentle incoming swash, and away from the beach with a receding swash, and sometimes the valves are overturned (Figure 14).

Water movement on the beach is infinitely more complex than in the flume where, for example, the water moved only in one direction. On the beach the swash flows in two principal directions, first towards shore and then away from it, but usually it does not follow the same path in and out. Successive swashes do not always come from the same direction, nor are they evenly spaced. The shells during the beach test became oriented in more or less the same manner as when they were in the flume, in part, because they were exposed only to the incoming swash and, in part, because the water velocities were not high. At high velocities, such as those observed by the senior author after a hurricane, shells roll end over end in the swash zone. An excellent discussion on the effect of swash moving obliquely up and down the beach on shell orientation and sorting is given by Lever (1958).

Behavior of Shells Progressively Covered by Water

Buoyant force increases as shells are progressively covered by water because more and more water is displaced. Observations were made of shells of *D. robustum* and *A. brasiliana* progressively covered by water both in the swash zone and in the laboratory, where shells were placed inside beakers which were then slowly filled with water. Air escaped from beneath the shells when they were about half covered by water. Air escape culminated with the release of a large bubble from beneath the dorsal edge of the shell. The plane of commissure of shells of *D. robustum* formed an angle of about 80° with the horizontal at the time the large bubble was released. Many shells of *D. robustum* overturned apparently due to the pushing action of the released bubble. Those shells that did not overturn, but returned to the bottom after the release of the large bubble of air retained some of the original air beneath them. No further air was released with further increase in water level. The volume of air trapped beneath two *D. robustum* shells was measured after they settled to the bottom. One shell contained 19 cc or 18.2 per cent of the original volume of entrapped air; the other shell contained 8 cc or 16.3 per cent of the original entrapped air. The volume of air retained beneath the shell is sufficient to materially increase the shell's buoyancy. Shells of *A. brasiliana*, which are heavier than shells of *D. robustum* of the same size, did not overturn.

The importance of the buoyant uplift of entrapped air in overturning valves may be reflected in the relative proportions of values of *D. robustum* and *A. brasiliana* deposited on a beach. In a collection of *D. robustum* shells cast upon the beach of Mustang Island

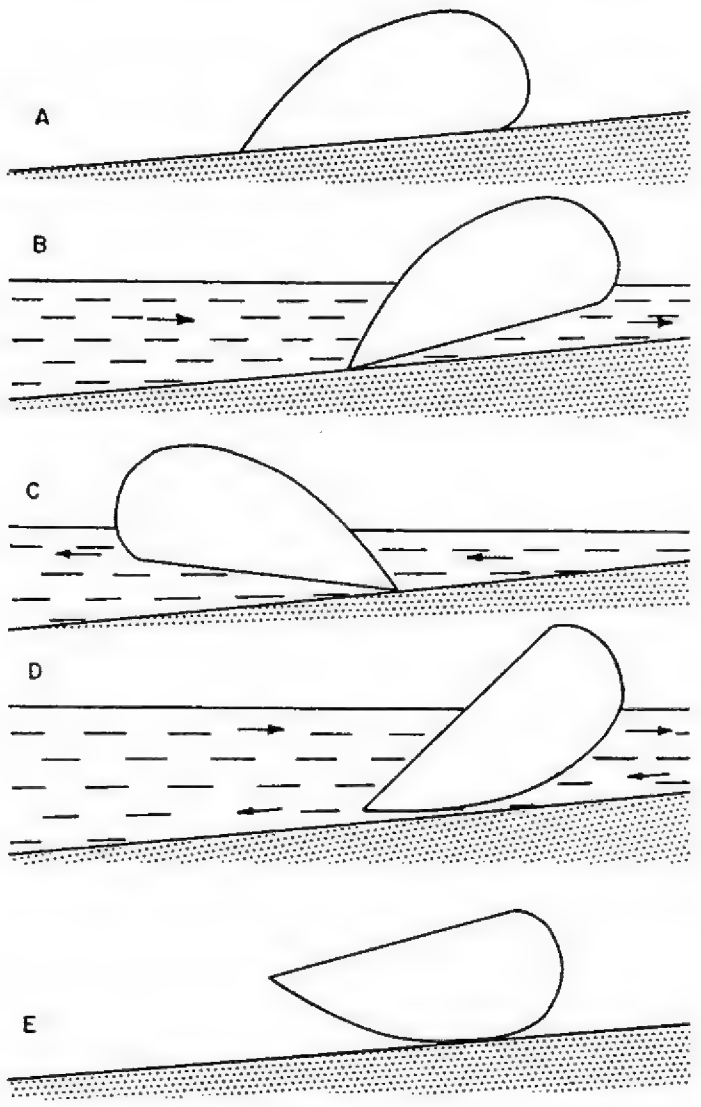

FIG. 14. Behavior of *Dinocardium robustum* shell observed on the beach of Mustang Island, Texas. A, original position and attitude of shell above waters edge. B, encompassed by incoming swash with air entrapped beneath the shell raising the beak. C, outgoing swash turns shell with ventral edge as pivot. D, incoming swash overturns shell. E, final position and attitude of shell on beach.

within a 24 hour period 65 per cent (82) were concave upward. On the other hand, shells of *A. brasiliana* are usually found convex upward, *e.g.*, in a collection of 95 shells made along the water's edge of Mustang Island, 85 per cent were found convex upward.

In deeper water both species usually occur in a convex upward position. In 10 trials in water 20 cm deep, two specimens of *D. robustum* placed concave side up on the sand surface averaged only seven seconds in this position before turning over. When the procedure was reversed and the specimens were placed on the sand convex upward, all valves were in the same position at the end of one minute's observation. However, in the interim each specimen had turned completely over (360°) an average of one time. The valves remained more or less in the same place during the observations. The fact that single pelecypod shells are more stable with the concave side down and are usually found in that position is well known (Shrock, 1948, pp. 313–320). The present observation suggests that single valves acted upon by currents turn over and over, remaining a short time in the concave upward position and a considerably longer time in the concave downward position. At any given time more valves would be in the concave down position than in the concave up position.

The Effect of Naturally Bored Holes on Shell Transport

Holes in shells are formed in nature by boring snails, boring sponges, boring algae, boring fungi, worms, and by abrasion or breakage. The per cent of shells with holes is

sometimes a considerable part of the total shell accumulation, *e.g.*, 88 per cent of dead shells belonging to the pelecypod *Spissula elliptica* collected along some coasts have been bored by the snail *Natica alderi* (Twenhofel and Schrock, 1935, p. 359). In conjunction with the present study the authors tabulated the number and probable cause of holes in a collection of shells from a Gulf of Mexico beach near Progreso, Yucatan Peninsula, Mexico (Table 3). Snail-bored shells of brachiopods have been reported from as far back as the early Paleozoic (Bucher, 1938). Boring sponges have an equally long range.

Holes made by boring sponges, algae, fungi, worms, and some snails are extremely small. No escape of air was evident when shells with considerable sponge borings were emersed convex upward under water. Air readily escaped from larger holes caused by abrasion or breakage but small holes apparently do not allow passage of air.

Snail-drilled holes vary considerably in diameter and position on the drilled shell. Air does not readily escape from snail-drilled holes having a small diameter. The position of a snail-drilled hole also affects the volume of air entrapped beneath the shell, because air above the hole is retained. For example, the volume of air retained beneath several snail-drilled shells of *A. brasiliana* was measured and found to vary from about 39 to 59 per cent of the internal volume of the shell (Table 4). Velocities obtained in flume experiments using snail-drilled shells were quite variable and higher than obtained with artificially drilled holes, probably because of air retained beneath the snail-drilled shells.

It is conceivable that shells with holes might accumulate in one place on a beach and shells of similar size without holes in another. Bucher (1938) found many snail-drilled shells of the brachiopod *Dalmanella meeki* (Miller) in a thin shale of Upper Cincinnatian age, although snail-drilled shells were rare elsewhere. This may have been the result of differential sorting.

Conclusions

1. The force required to move shells is directly proportional to the normal component of the weight of the shell. Air entrapped beneath a clamshell decreases the normal component of the shell weight so that it can be moved by a smaller force.

TABLE 3

Statistics on the number and cause of holes in two common species of pelecypods collected from a beach near Progreso, a seaport town on the Yucatan Peninsula, Mexico

Species	Total number collected	Percent with hole	Percent perforated by sponge	Percent drilled by snail	Percent with hole eroded
Arca zebra	156	66.6	56.2	1.7	8.7
Chione cancellata	118	27.5	13.2	14.3	0

TABLE 4

Volume of air entrapped beneath valves of *A. braziliana* containing holes drilled by snails

Type of valve	Hole diameter cm	Hole position	Cup volume cc	Air entrapped cc	Approximate percent of original air remaining under shell
Left	0.20	umbo	9.4	5.6	59.5
Left	0.15	umbo	2.8	1.0	39.7
Left	0.20	umbo	5.4	2.1	39.0
Left	0.12	umbo	0.8	1.0	.....

2. Effective density of a shell is a major factor affecting ease of shell transport. The distance a shell is moved by a given competent current varies inversely with the square root of the effective density of the shell.

3. One reason small shells are transported farther than large shells in the swash zone is because small shells are covered by a relatively greater proportion of water relative to their mass, and, therefore, have lower effective densities when exposed to swash water of the same depth. Shells are probably more easily sorted according to size by currents in the beach environment than when they are completely submerged.

4. Shells with holes lag behind shells without holes which are buoyed with air.

5. Air entrapped beneath shells plays an important role in the complex of factors determining the orientation of shells deposited on the beach.

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Studies of Oxygen Metabolism of Streams of North Carolina[1]

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Abstract

Diurnal measurements of dissolved oxygen were made in the Neuse River and eight other streams in the mountains, piedmont, and coastal plain of North Carolina. The data were used to estimate gross photosynthesis and total respiration of the streams. Production rates were 0.3 to 9.8 gm/m²/day oxygen; respiration rates were 0.7 to 21.5 gm/m²/day. Respiration was much in excess of photosynthesis at all stations indicating the aquatic communities were deriving as much organic matter from the land drainage as from photosynthesis within the streams. Metabolism in riffles was greater than in pools. In the Eno River a ten fold range in metabolism was observed between low values of late winter and high values of late spring. Streams draining forest and agricultural lands of North Carolina are intermediate in fertility as compared to other aquatic environments.

Introduction

Relatively few studies have been made of the metabolism of streams. Most studies are for specialized types of flowing water such as springs and polluted rivers. As reviewed by Odum (1956), the available data on flowing waters suggested relatively high rates of gross photosynthesis and total community respiration. Subsequent study in an experimental stream microcosm (Odum and Hoskin, 1957) verified the important role of current in stimulating high rates of metabolism by recirculating chemical nutrients.

Yet, few efforts have been made to appraise the photosynthesis and respiration of ordinary streams which drain forests and agricultural lands. In order to characterize the metabolism of such streams, free-water oxygen methods for the measurement of metabolism in flowing waters were applied to stream stations representing three major land regions: the mountains, the hilly piedmont, and the flat coastal plain of North Carolina. Eight stations were selected to outline the pattern of metabolism from the headwaters to the mouth of the Neuse River, which is a small representative river of the Atlantic coastal area of the southern United States.

Methods

In order to estimate stream metabolism, measurements of oxygen content were made in the streams at regular three-hour intervals throughout 24-hour periods. Water samples were collected in triplicate in 150 ml glass stoppered bottles.

Gross primary production and total respiration were estimated graphically from rates

[1] From a thesis submitted to Faculty of Duke University in 1957 as part of the requirement for the Masters Degree in Zoology under the supervision of Dr. Howard T. Odum and Dr. Dan Livingston. The study was aided by a grant from the National Science Foundation, NSF G1849.

of oxygen change after corrections were made for the exchange of oxygen between the water and the atmosphere. These methods are described elsewhere (Odum, 1956; Odum and Hoskin, 1958).

Dissolved oxygen was measured with the unmodified Winkler method when tests with the Ohle method indicated little or no interfering substances (Ohle, 1953). When the Ohle test indicated interfering substances with an effect greater than 0.3 ppm, a correction was added based on the test.

In part of the series diurnal measurements were made at two stations, one about a mile upstream from the other. When the oxygen values at the two stations were similar, the values were averaged as if they were duplicate samples from the same water mass with similar metabolism.

Temperatures were measured at each sampling so that the per cent saturation could be determined. For stations at high altitude, saturation values were obtained from Rawson (1944). All of the diurnal curves and temperature data are contained in the unpublished thesis (Hoskin, 1957).

Oxygen Metabolism in the Neuse River System

The Neuse River (Figure 1) rises from small tributary creeks near Durham, North Carolina in the clay-covered hills of the piedmont area, a geologically ancient, metamorphosed region. The tributaries studied are the Little River, the Eno River, and Sandy Creek. Data on the streams are given by Harris and Joyner (1953–1954). The waters are soft (28 ppm calcium carbonate hardness), slightly acid (pH 6.5), with high turbidity of suspended clay. As the waters flow seaward past small towns, small

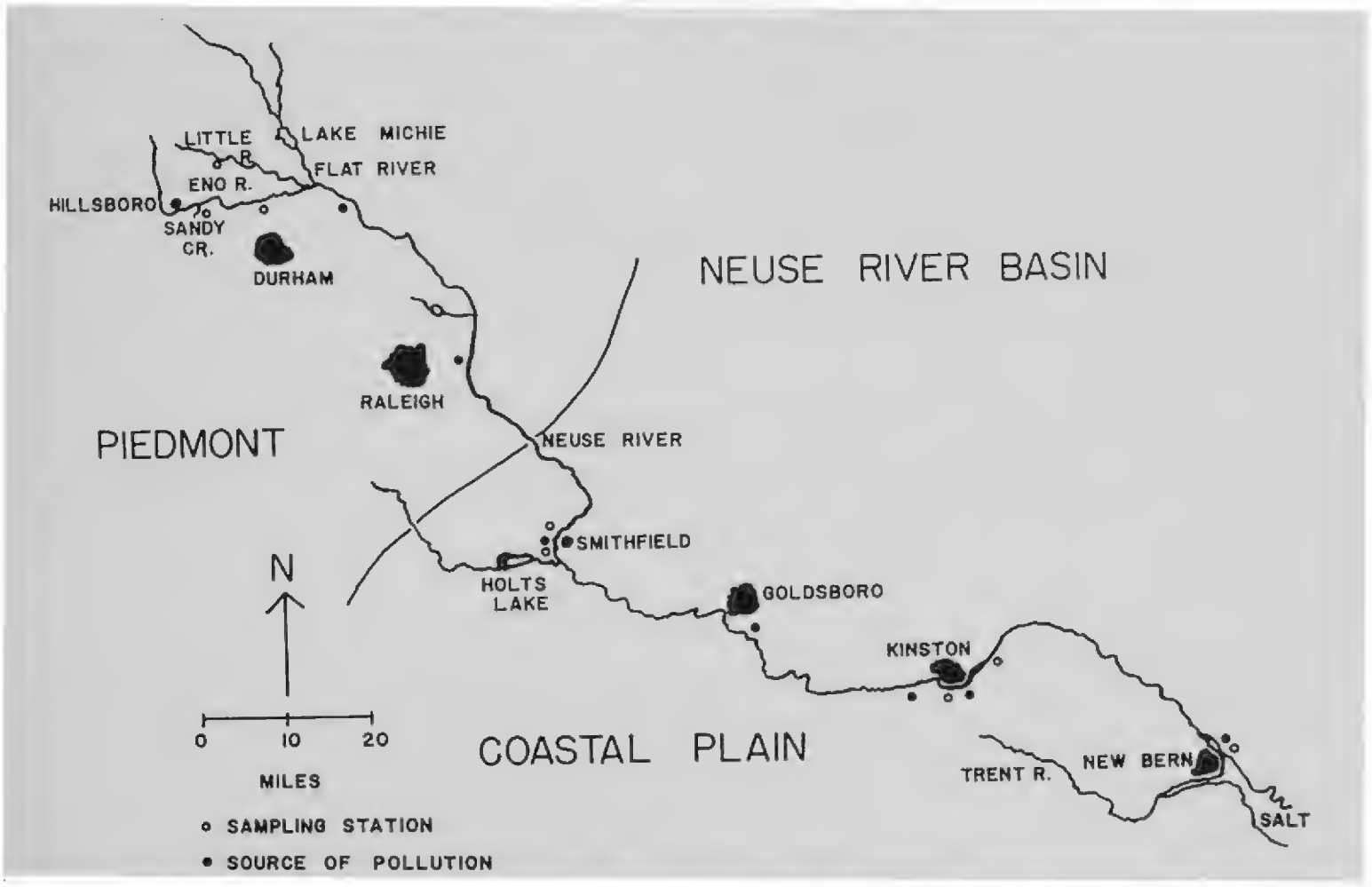

FIG. 1. Neuse River System of eastern North Carolina. Sampling stations and some sources of minor pollution are indicated.

amounts of partially treated municipal wastes enter the stream. Just below Raleigh, North Carolina (Figure 1), the stream crosses from the piedmont to the flat sediments of the coastal plain, over Cretaceous formations first and then to younger strata and, finally, into salt water estuaries at New Bern, North Carolina. Especially below the fall line (piedmont-coastal plain boundary), the flow is sluggish and the water is deeper.

Typical diurnal oxygen curves were obtained in the Neuse River in the winter and summer. Oxygen was minimal late at night rising to a maximum with photosynthesis late in the day. A representative curve for the shallow headwaters is given in Figure 2 for Sandy Creek, an unpolluted brook draining forests and fields near Duke University. Partially shaded by trees, much of the photosynthesis and respiratory metabolism are on the bottom. The waters, only 0.3 m deep, were undersaturated during the entire period in spite of considerable diffusion of oxygen into the stream. When the diffusion was subtracted, a typical, bell-shaped curve for photosynthesis was obtained (as indicated by the black circles on the lower part of Figure 2). Photosynthesis was only one-third of the total respiration.

In Figure 3, data are reported from the Neuse River at Kinston, North Carolina. The curve is representative of those in the sluggish, deeper waters of the river in the coastal plain region. Although there is little diurnal change in concentration of oxygen (expressed in ppm), the water column is deeper so that a small change in oxygen concentration indicates a fairly large total oxygen metabolism under a square meter of the surface. The agreement between replicate oxygen samples indicates continuous mixing. As in the

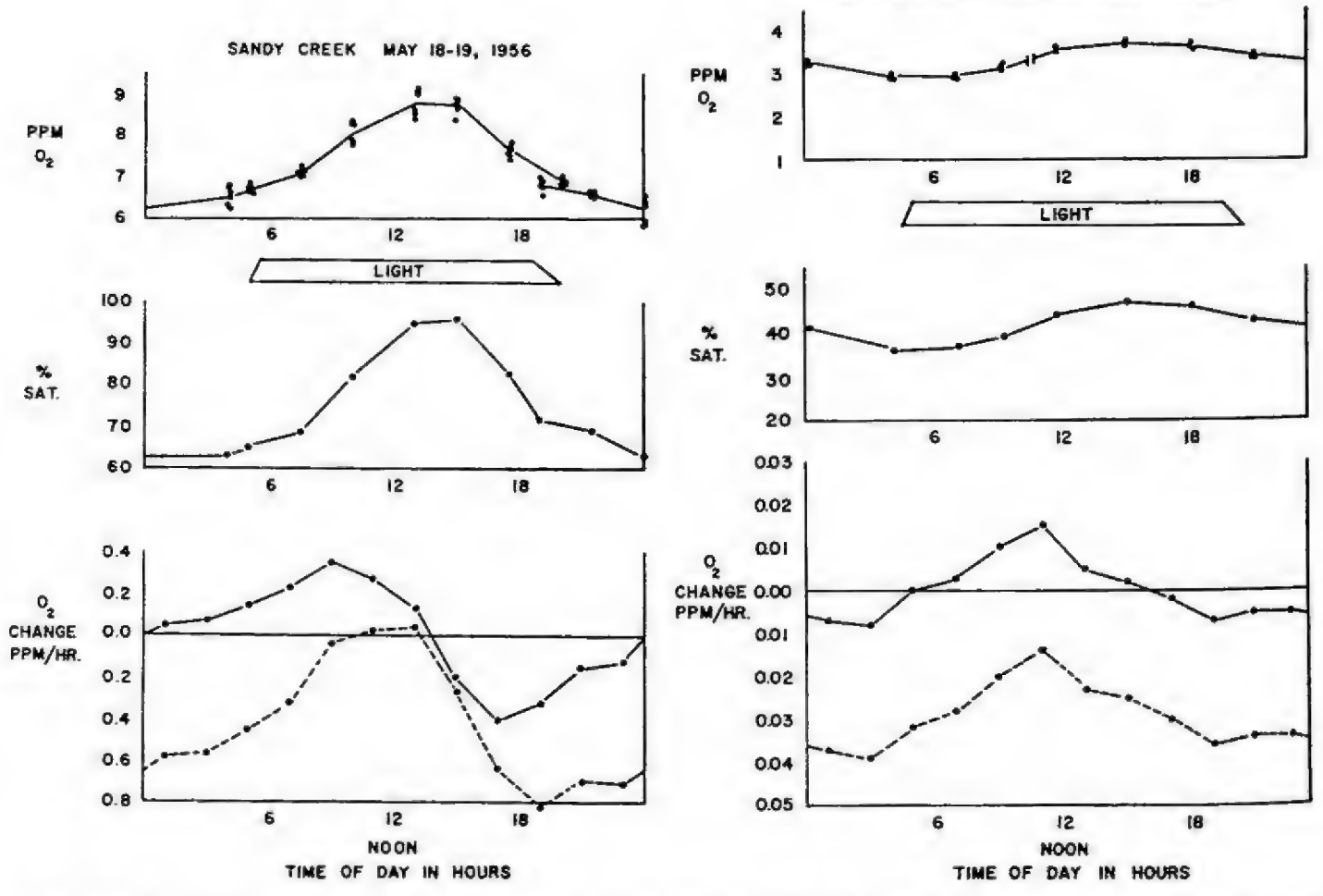

FIG. 2. Diurnal oxygen data from Sandy Creek, May 18–19, 1956, a brook draining the Duke Forest near Durham, North Carolina. The rate of change graph computed from the oxygen curve is plotted with open circles; the graph of photosynthesis and respiration which results after subtraction of diffusion exchange is plotted with solid circles.

FIG. 3. Diurnal oxygen data from the Neuse River at Kinston, August 8–9, 1956. Symbols are described in the legend for Figure 2.

headwaters, the stream remained undersaturated throughout the day. Little light could penetrate through the average two meter depth to the bottom of the relatively turbid water.

Data for other stations, based on curves like those in Figures 2 and 3, are given in Table 1. At all stations respiration exceeded photosynthesis. The diffusion constants

TABLE 1

Oxygen metabolism of North Carolina streams

Stream and location	Depth in meters	Date 1956	Diffusion constant (K) in gm oxygen/m^2/hr. at 0 percent saturation	Metabolism gm $0_2/m^2$/day		
				P	R	P/R
Neuse River System						
Sandy Creek, Durham	0.26	May 18–19	0.45	1.32	4.10	0.3
Eno River, Durham	0.65	June 11–12	0.98	2.40	5.63	0.4
Little River, Durham	0.6	July 11–12	0.85	1.28	5.56	0.2
Neuse River, Smithfield	1.0	July 19–20	0.10	1.75	2.40	0.7
Neuse River, Kinston	2.0	Aug. 8–9	0.10	0.29	1.68	0.2
Neuse River Estuary, New Bern*	2.5	Aug. 21–22	4.20	9.8	21.5	0.5
Other Streams						
Sinking Creek, Virginia	0.4	May 30–31	1.55	9.36	17.20	0.5
Stirrup-Iron Creek, Wake City	0.3	June 18–19	0.12	0.52	1.88	0.3
Little River, Allegheny City	0.5	Oct. 13–14	2.00	1.24	5.27	0.2

* Strong wind and tidal current, one mile wide

computed from the curves were within the range found in other streams (Odum, 1956). The rates of daily photosynthesis were relatively small, only one-tenth of that found in some clear, spring waters. Respiration rates (although somewhat greater than photosynthesis) were much less than those found in heavily polluted waters or fertile natural communities.

The constant excess of respiration over photosynthesis indicates that the biotic community of the stream system receives more organic matter than it produces. Therefore, the overall metabolism may be classified as heterotrophic.

The diurnal curve at New Bern was obtained from a bridge over the salt water Neuse estuary at a point where it is one mile in width. The high value of the diffusion constant may have been caused by strong tidal currents and strong winds. This value is only approximate because no record was made of salinities during the period so that per cent saturation values used in the calculation were only approximate. The relatively high values for photosynthesis and even higher values for respiration are similar to some reported from fertile estuaries in Texas (Odum and Hoskin, 1958).

COMPARISON OF POOL AND RIFFLE

Calculations of metabolism in the Eno River, a headwater tributary of the Neuse, were made with data from two contrasting stations as reported in Table 2. One station was just below a pool, unshaded, 0.75 m deep, with the bottom covered with silt; the other station was at the foot of a riffle, shaded by overhanging trees, 0.2 m deep, with the bottom covered with granite boulders.

Neither station completely represents the river metabolism since the water is continually passing through an alternating sequence of pools and riffles. As calculated in Table 2, computations were made as though the water were a stationary mass or flowing into a

TABLE 2

Calculations of stream metabolism at two contrasting stations in the Eno River, Durham County, North Carolina in 1957

Date 1957	Metabolism in gm oxygen/m²/day				
	Productivity			Respiration	
	Pool	Riffle		Pool	Riffle
February 16–17	0.13	0.42		0.79	0.89
February 23–24	0.75	1.00		1.15	1.68
	.....	.....	Rain	.....	.....
March 30–31	1.26	1.14		1.44	1.44
	.....	.....	Rain	.....	.....
April 13–14	0.41	....		0.72	....
April 20–21	2.61	6.25		3.36	8.76
April 27–28	5.21	5.74		11.95	13.20
	.....	.....	Rain	.....	.....

station with the same history as the water flowing out. The correct values for the metabolism of the stream may lie between the results given in the table.

Although neither of the values are precise estimates of metabolism, the generally higher values found below the riffle (in spite of the shade) suggest a higher metabolism in the riffle section as compared to the pool zone.

SEASONAL CHANGES IN THE ENO RIVER

The diurnal measurements of metabolism in the Eno River were made in late winter, through the spring season (Table 2), and in the summer (Figure 4). As conditions of light and temperature changed with the coming of spring the initially low production and respiration rates increased almost 10 times. As in the other stream stations studied,

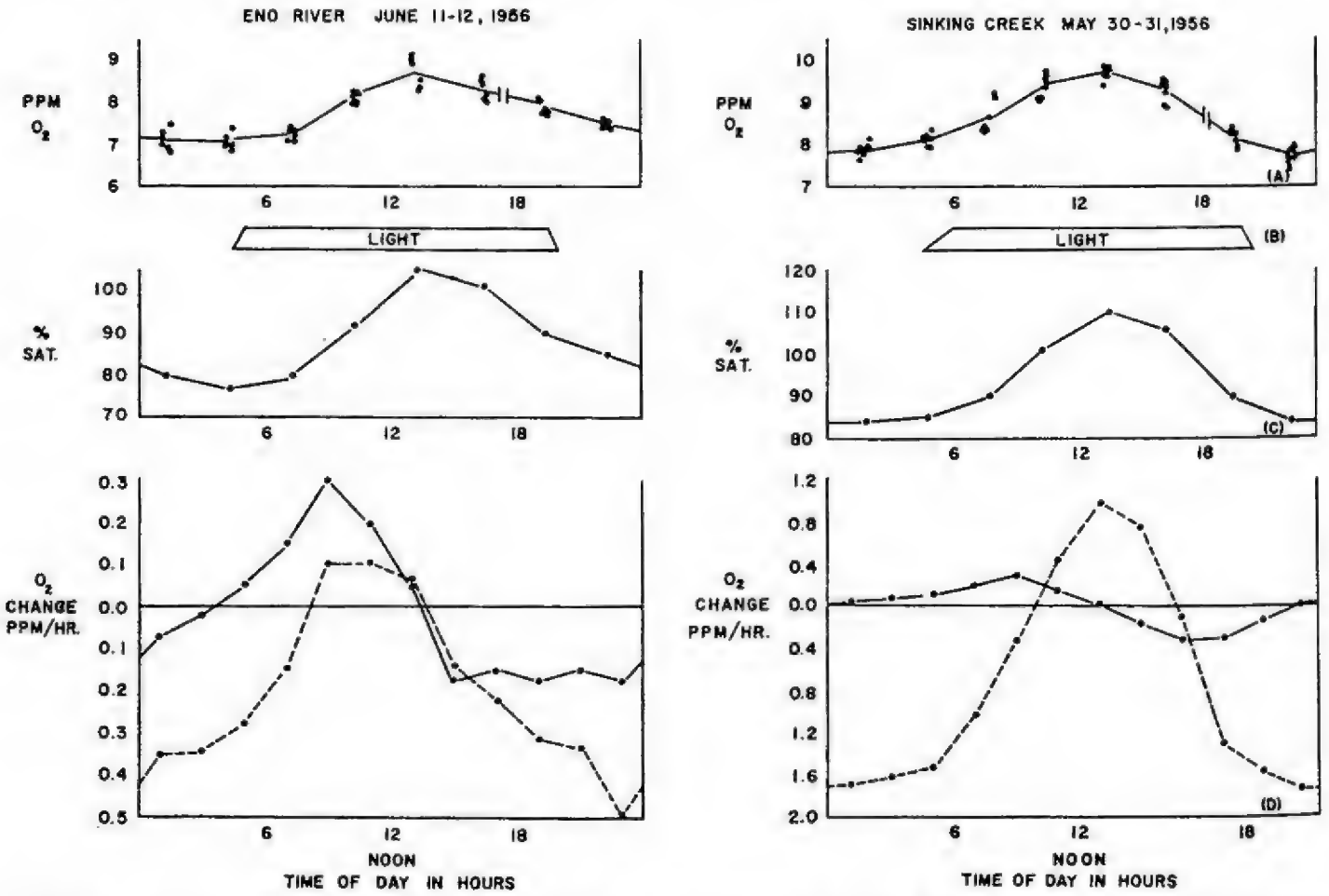

FIG. 4. Diurnal oxygen data from the Eno River tributary of the Neuse River, June 11–12, 1956. Symbols are described in the legend for Figure 2.

FIG. 5. Diurnal oxygen data from Sinking Creek, the stream near Mountain Lake, Virginia, May 30–31, 1956. Symbols are described in the legend for Figure 2.

respiration exceeded photosynthesis. A factor contributing to low photosynthesis in early spring was the turbid high water conditions that existed for several days following spring rains.

Mountain Streams

Data on two mountain streams are given in Figure 5 and Table 1. With relatively swift currents, diffusion constants were relatively high. Sinking Creek, near the biological station at Mountain Lake, Virginia, in a mountain valley drains a region with limestone sink-holes and valley farms. A rich biota and hard waters are indicated by Burton and Odum (1945). Data in Figure 5 were taken at three stations about one-half mile apart which included a rapids zone and a zone of placid flow. All points were averaged to obtain a curve for the whole stream. The daily photosynthesis of 9.4 gm and the daily respiration of 17.2 gm (Table 1) indicate high fertility which is consistent with the fertile and soluble substrates drained.

In contrast to Sinking Creek is the Little River, Allegheny County, N. Carolina, which drains insoluble igneous rocks. On October 13, metabolism was small. Production estimate by McConnell (1959) for mountain streams in Utah are within the range of the North Carolina measurements.

An effort was made to measure metabolic rates in Little Stony Creek, Virginia, a cold, shaded headwater stream that flows downward in nearly continuous rapids. Here the diffusion rates were so large that the effects of stream metabolism on the oxygen content were completely masked. McConnell (1959), studying a river of like gradient, described similar difficulties.

Comparison with Other Waters

Even where diurnal changes of temperature were relatively large, a distinct increase in oxygen was observed during the day associated with light and photosynthesis. Thus, these diurnal curves were different from those obtained in Afon Tuen, Wales, September 30, 1940, by Laurie (1942); in which diurnal temperature changes accompanied by rapid exchange with the atmosphere produced daytime minima and nighttime maxima.

The metabolic rates reported in this paper from ordinary streams of North Carolina (P, 0.3–9.8 gm/m^2/day; R, 0.7–21.5 gm/m^2/day) are generally lower than those of many polluted streams and mineral springs in which metabolic rates of 20 to 60 gm/m^2/day have been reported (Odum, 1956). However, these streams have higher production and respiration rates than those reported for most oceanic waters and many lakes.

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The Hydrography of the Inshore Northeastern Gulf of Mexico[1]

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Abstract

Thirty sampling trips were made to a distance of twenty-eight miles into the northeastern Gulf of Mexico from Alligator Harbor, Franklin County, Florida, in 1954. Water temperature, salinity, and light penetration were measured. Temperatures in the inshore waters ranged from 14°C to 30°C. Hydrographic profiles gave evidence of intense local cooling in the spring. Density inversions were present on several occasions. The local salinity pattern of the inshore waters was controlled by stream flow, particularly that of the Apalachicola River. Minimum salinities were found in March and were correlated with high stream flow. Maximum salinities occurred in mid-August.

Introduction

As a basis for a study of productivity of a semitropical, marine area, an investigation was made of physical, chemical, and climatological conditions of a shelf area of the northeastern Gulf of Mexico. The hydrographic results are reported here. The area investigated is bounded on the south by a line connecting Cape San Blas, Florida, with the mouth of the Steinhatchee River, Florida (Figure 1). The coastal features and general benthic topography may be found on United States Coast and Geodetic Survey Chart 1261. The base of operations was the Marine Laboratory of the Oceanographic Institute located at Alligator Harbor, Franklin County, Florida.

Acknowledgement is due to Dr. Harold J. Humm and Dr. F. C. W. Olson for their interest, encouragement, advice, and readiness to provide facilities. Drs. Samuel Meyer and Dale F. Leipper provided funds and assistance when most needed. Messrs. George D. Grice, Jr., Tim Murphy Smith, Murice O. Rinkel, and James Thomas cooperated on many of the sampling trips, and much of the data presented here was collected with their help. A National Science Foundation Fellowship provided financial assistance during the years 1954–1956.

Methods

Sampling trips were made on the average of twice a month in a southerly direction, 160° to 180° true bearing from Alligator Harbor. The maximum distance from shore of the stations was 28 miles. Stations were spaced at five mile intervals in a straight line. At each station water samples were obtained at three or more depths with a Kemmerer water sampler. The area sampled is shaded in Figure 1.

[1] Contribution No. 113 from the Oceanographic Institute, Florida State University, Tallahassee. Modified from a dissertation submitted to the Graduate School, Florida State University, in partial fulfillment of the degree of Doctor of Philosophy.

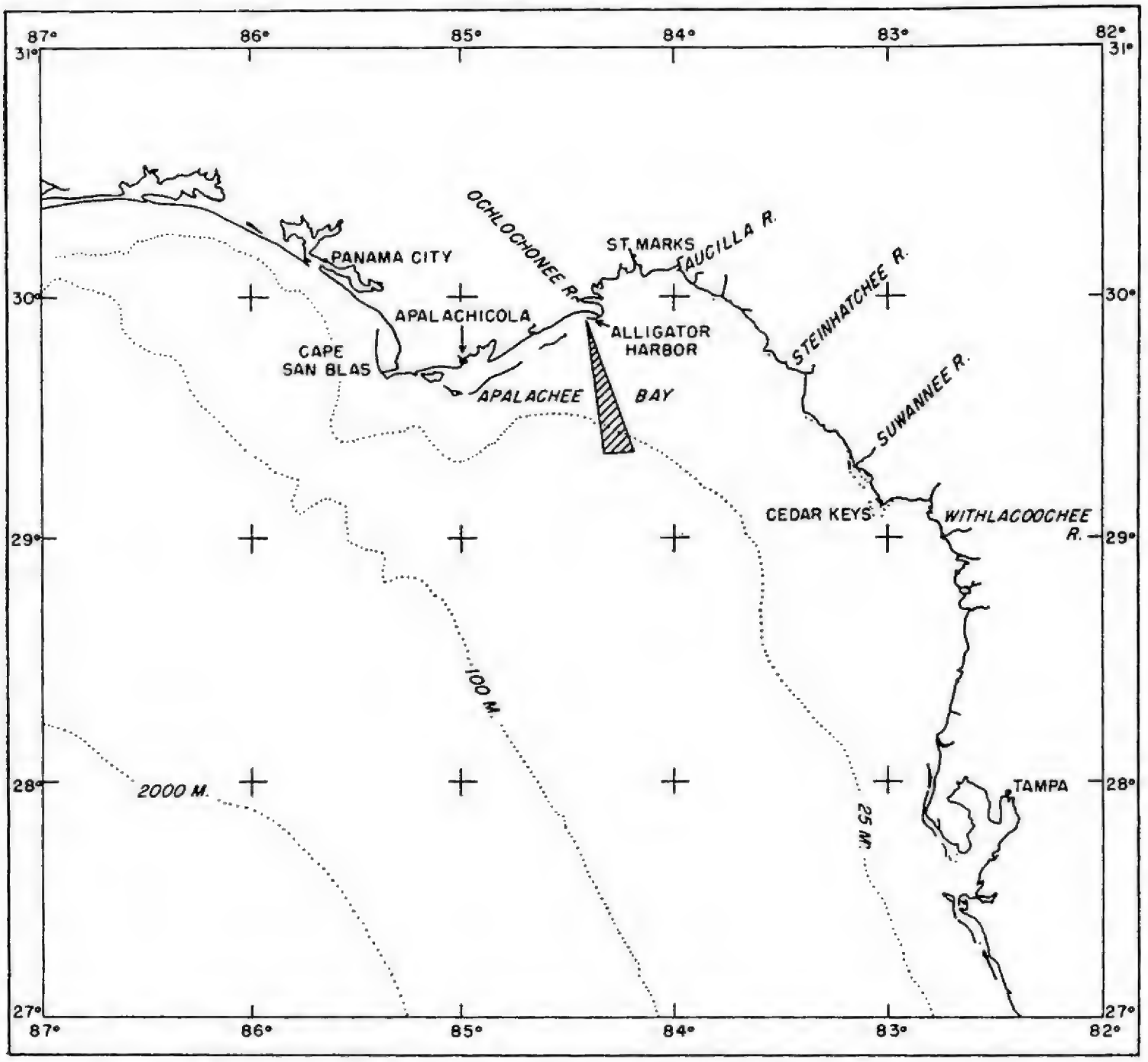


FIG. 1. Northeastern Gulf of Mexico. The hatched sector indicates the area sampled.

Specific gravity by hydrometer was determined in the laboratory and converted to equivalent salinities by nomogram (Olson, 1956) or tables (U.S. Coast and Geodetic Survey, 1953). Salinity hydrometers were considered, conservatively, to have an accuracy of ± 0.5 ppt. In drawing isolines, values have been rounded to the nearest 0.5 ppt.

Temperatures *in situ* were taken with a 200 foot bathythermograph. The slides, plus one set of prints, are on file at the Oceanographic Institute, Alligator Harbor, Florida.

Water transparency was measured with a 20 cm Secchi disk and a submarine photometer. The extinction coefficient, "K", for the photometer was computed from the formula.

$$K = \frac{2.303}{R_{10}} \tag{1}$$

where R_{10}, the decimal reduction depth, is the depth at which 10 per cent of surface illumination occurs. The Secchi disk extinction coefficient, "K", is defined by

$$K = \frac{1.7}{D} \tag{2}$$

where D is the disappearance depth in meters (Poole and Atkins, 1929). This conversion factor was confirmed by calibrating the disk against the photometer. The factor for offshore water was 1.68. However, in Alligator Harbor a factor of 1.43 was computed by Sipple (quoted in Olson, 1955, p. 88).

Description of the Region

The Florida peninsula and the continental plateau out to the 300 foot contour comprises the Floridian Plateau. The recent sediments include quartz sand mixed locally with shell and shelly sand. Sand and silt are being deposited on tidal flats, bars, and flood plains. Exposures of Ocala, Suwanee, and Tampa limestones occur in that order from Cedar Key to Ochlockonee Bay, where the rock stops abruptly, marking the east boundary of the Apalachicola Delta.

The coast to the west of the Ochlockonee River is alluvial; to the east it is a drowned limestone plateau. Between the Ochlockonee River and Cedar Key the vegetation is low *Juncus* marsh with wooded swamps to the rear. From the river westward to Cape San Blas, the shore is sand beach with shoals, spits, barrier islands, and offshore bars. A prominent feature of this section is the Apalachicola River, the largest in Florida. In addition to the Ochlockonee and Apalachicola rivers, the Aucilla, Steinhatchee, and Suwanee rivers all add their contents to Apalachee Bay (Figure 1).

The bottom typography along the transect of stations has been discussed by Curl (1957).

Hydrographic Results

Salinity

Salinity measurements were made throughout 1954 and during early 1955 (Figures 2 and 4). Averages of water columns, referred to three standard stations, are presented in Figure 2a. The stations are "shoal" from the shore out to four miles; "inshore" from four to 12 miles out; and "offshore" from 12 to 30 miles out.

There is a wide range in values and the average salinity is high. The same data are plotted in Figure 2b. The ordinate represents the distance from shore, and time is plotted on the abscissa.

In January, 1954, salinities were relatively high near the coast and gradually decreased during February and early March. A minimum was reached at all stations in late March. The salinities then increased until a maximum was attained in mid-August when 36.0 ppt water came within five miles of shore. A secondary decrease in October and November displaced the 36 ppt isohaline 10 miles seaward. There are several minor fluctuations in shoal water imperfectly reflected at the other stations. Mixing is indicated by separated isohalines in mid and late March and again in mid-November.

Temperature

In Apalachee Bay the inshore water had an annual range of 15°C; the offshore water a range of 14.5°C. The graphs of surface and bottom water temperatures are similar in appearance (Figure 3). The greatest difference between inshore and offshore temperatures occurred in April: 5.2°C at the bottom and 3.2°C at the surface. The lowest temperatures encountered was 14°C inshore, at the surface in March. The highest tempera-

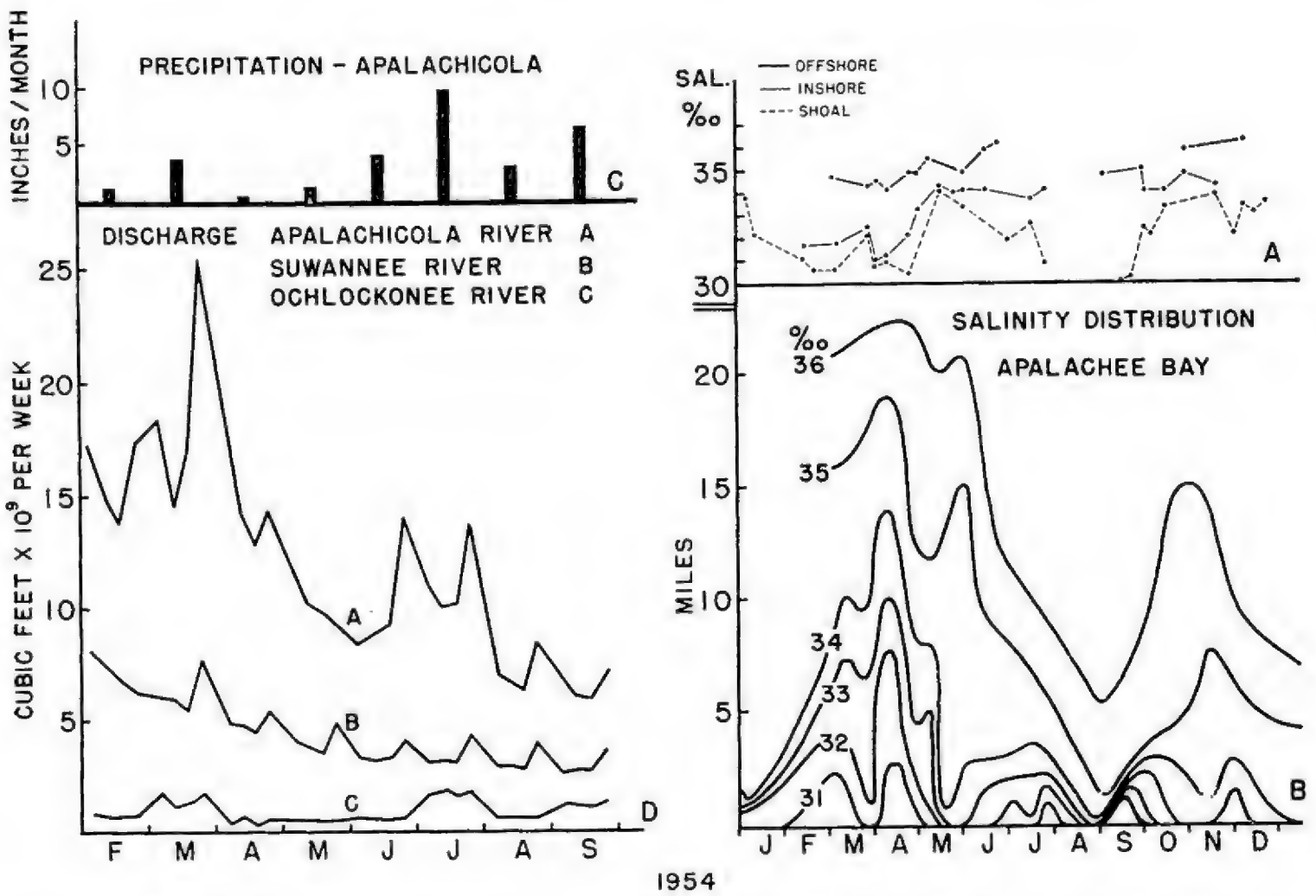


FIG. 2. Relationship between precipitation at Apalachicola, Fla., river flow of three Florida Rivers and salinity distribution in Apalachee Bay.

ture occurred inshore, at the surface, in July and August (30.1°C). The depression of inshore temperature in May was accompanied by sharp decreases in the daily minimum air temperature. In July the decrease in inshore temperatures was accompanied by a slight increase in stream flow of both the Ochlockonee and Apalachicola Rivers.

HYDROGRAPHIC PROFILES AND INVERSIONS

Profiles of salinity, temperature, and calculated density distribution for eight cruises have been plotted on Figures 4a to 4h. The profiles are selected for their individual interest but are generally representative of the period in which they were taken. A coefficient of stability, $E' = \frac{d\sigma_t}{dz} 10^3$ (Sverdrup, 1929; Sverdrup *et al.*, 1942, p. 417) has been computed for three meter intervals at selected stations and depths and has been plotted within circles on the profiles. A value of "0" represents indifferent stability, negative values indicate instability, *i.e.*, density inversions.

Stable conditions were found on March 5 and 26; April 2, 9, 23, and 30; July 14; September 1; and December 3. Unstable conditions were found on April 23, May 27, and September 1.

In very shallow water the position of vertical isopleths may be shifted by tidal water movements. It was calculated that the horizontal tidal displacement of an isopleth in the center of the profile is between 0.45 and 0.9 mile from a mean position.

The profile for March 5 (Figure 4a) depicts a condition which frequently occurs in this region. A convergence line consisting of a slick about 100 m wide along a true bearing of 280° was encountered nine miles from land. North of the line the water was

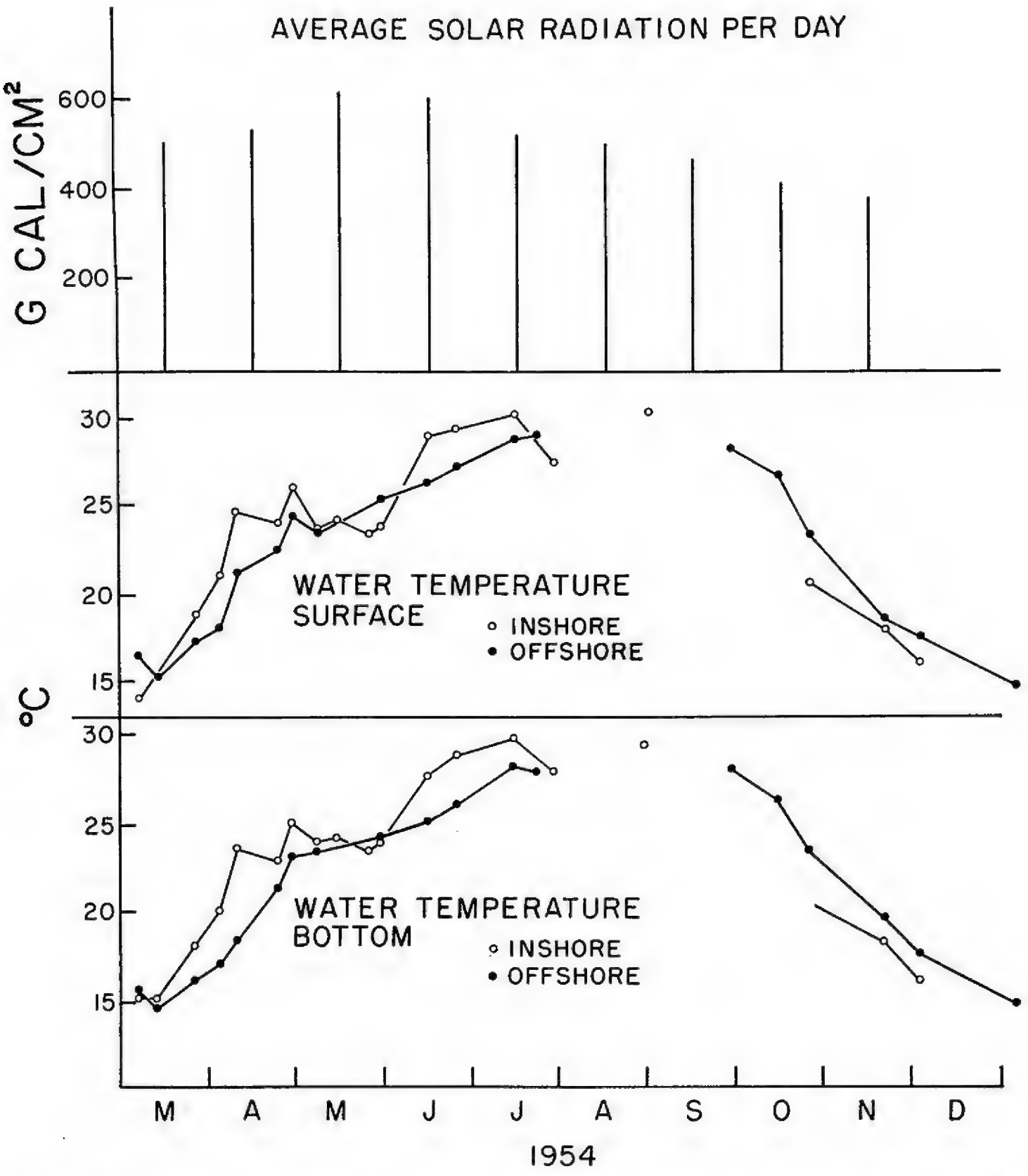
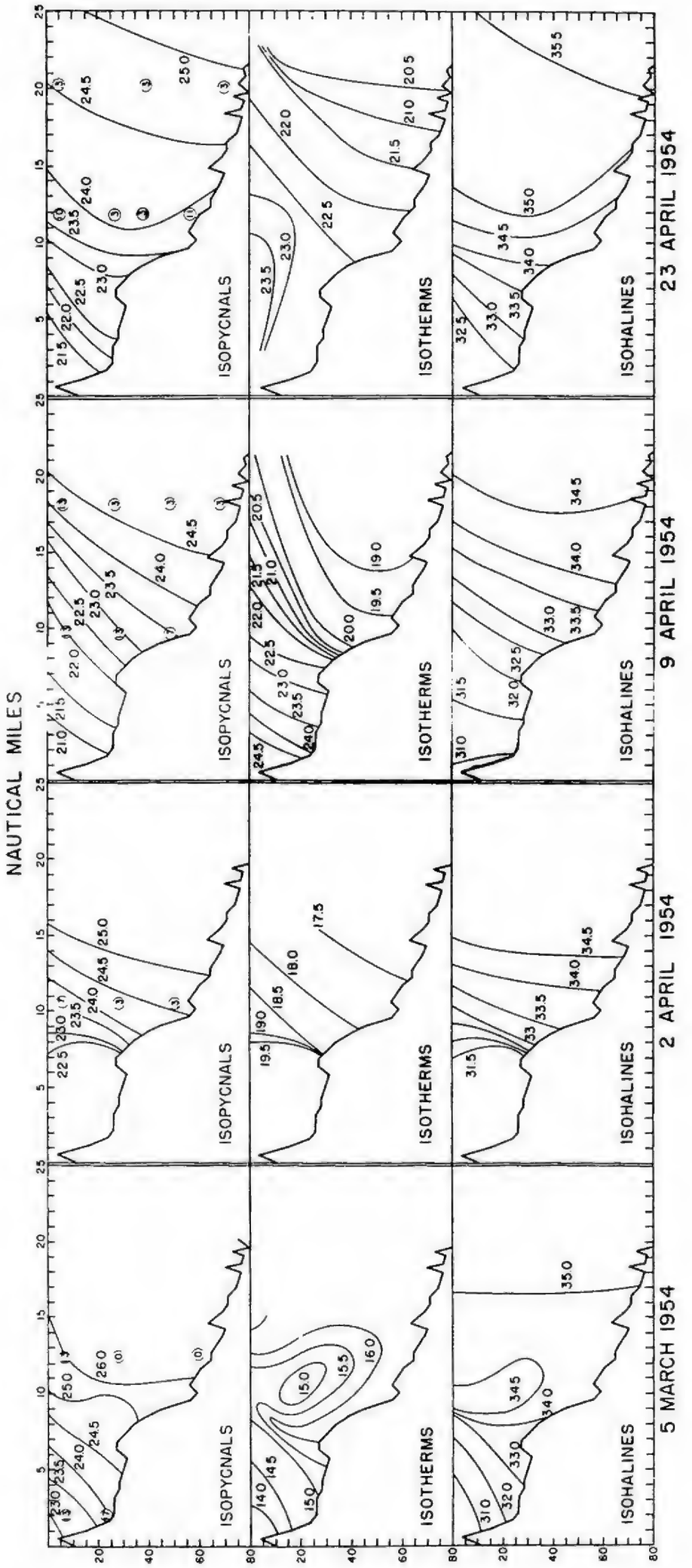


FIG. 3. Relationship of seasonal insolation at Apalachicola, Fla., and water temperature in Apalachee Bay.

turbid; in the line and to the south it was clearer. Numerous plant fragments, particularly of manatee grass, *Syringodium filiforme* Kutz. (*Cymodocea manatorium* Aschers), and turtle grass, *Thalassia testudinum* Koenig and Sims, were floating in the slick. The surface current velocity was 1.2 knots toward 270° true. The line was followed eastward until it curved south at the South Shoal whistle buoy.

The isotherms indicate the presence of an intrusive mass of cooler water partially cut off from water of the same temperature to landward. The salinity at the core of this mass was 2.5 ppt higher than the 15°C water to landward. The convergence line occurred at the landward boundary of the mass. Since the water in the mass was clearer and of higher salinity but not higher temperature than the shoal water, it probably originated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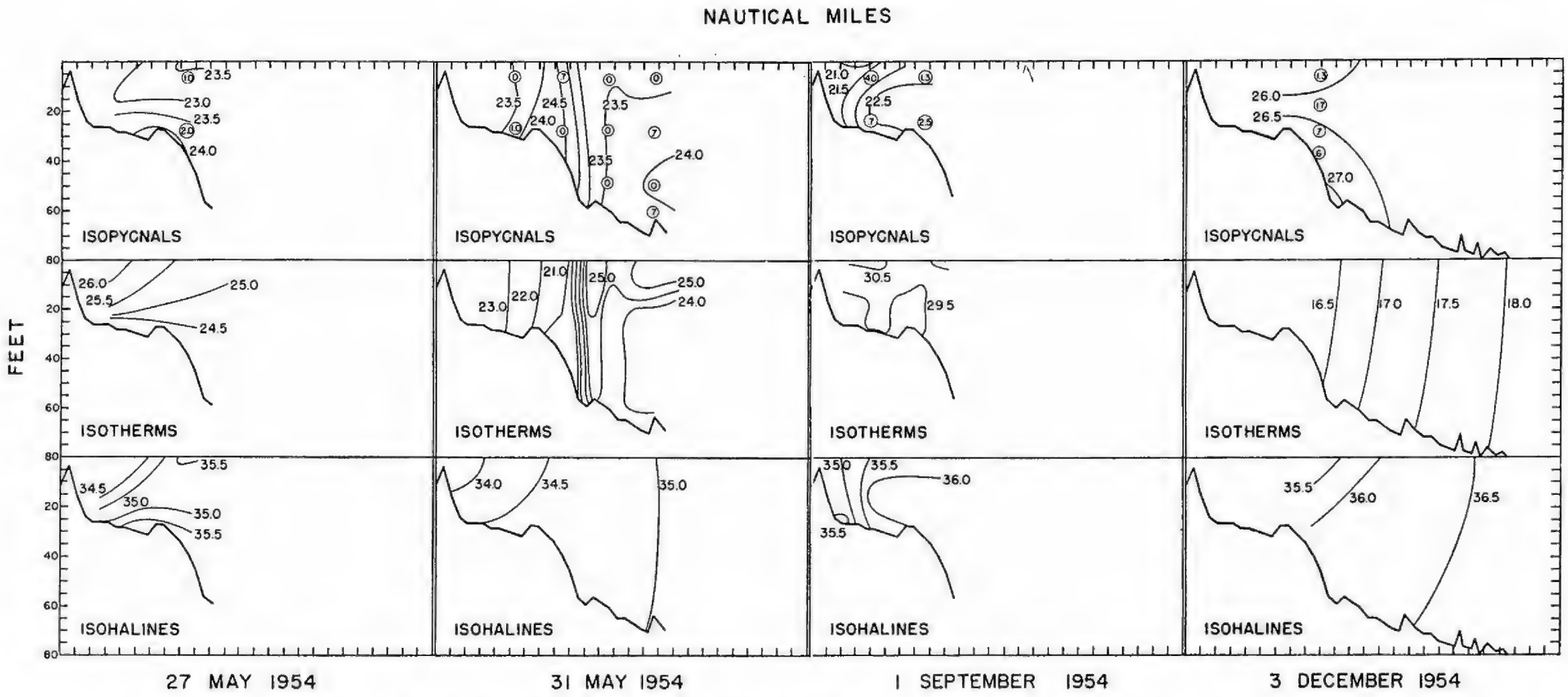

FIG. 4. Profiles of salinity, temperature, and density in Apalachee Bay in 1954.

in the shallower eastward portion of Apalachee Bay. There it acquired a lower temperature and subsequently sank on rounding South Shoal, producing a vertical wedge of 16°C water. The presence of much plant detritus, whose main source is also to the eastward, suggests a convergence mechanism.

During the cruise of April 2 (Figure 4b) estuarine water extended seven miles seaward. There were high river discharges during April. Seven days later, on April 9 (Figure 4c), the salinity distribution had not changed appreciably. The temperatures had risen several degrees along the entire profile.

On April 23 (Figure 4d) both salinities and temperatures had increased. The 35.0 ppt isohaline bulged landward at mid-depth producing a density inversion near the bottom. This may be an effect of tidal currents on sloping density discontinuities described by Ehrlich (1954). Ehrlich was able to show that subsurface inversions existed in conjunction with a boundary between light surface water from the Gulf of Maine and more dense slope water. The inversions were unstable according to Rayleigh's criterion and were shown to be produced by horizontal tidal currents. However, in Apalachee Bay, the total tidal excursion of a particle about a mean point is 1.2 ± miles, which may be too small to account for the magnitude of the inversions. It should be noted that mass transport along the axis of the bulge in the vertical plane is compatible with dynamic considerations (Sverdrup *et al.*, 1942, p. 504).

The distribution of physical properties continued relatively unchanged (except for the absence of inversions) until May 27 (Figure 4e). By then, cool, saline water had appeared inshore along the bottom. High salinity water also formed a layer offshore at the surface, possibly joining the deep water offshore. The result of this pattern was to produce a density inversion at the surface.

Four days later, on May 31 (Figure 4f), a very different situation prevailed. The inshore temperature had dropped by several degrees and the isopleths had become vertical. There was a very sharp temperature boundary nine miles offshore. Since March, 1954 the warmest water had been inshore. There had been two periods of cooling in May, with particularly low temperatures on the fifth and twenty-second of the month. On May 27 the effect of this cooling was not noticeable. River discharge was decreasing at this time, thus it would seem unlikely that cold, estuarine water was responsible for the inshore cooling. Moreover, the inshore salinities were not lowered from those of four days previous. The most plausible explanation of this distribution is that water in the shallow bay to the eastward had been subjected to local, very intense cooling and had then been moved westward, sinking. This is the same mechanism postulated for occurrences of March 5. The seaward side of the cold wedge presents a complex situation in which cool water has moved in from below, displacing warm water upward. At 10 miles, however, it appears that warm surface water has sunk alongside the cold wedge.

The cruises of June 15 and July 14 found the situation returned to normal with continued warming along the entire profile.

By September 1 (Figure 4g) high salinity water (36.4 ppt) had approached within four miles of land. The arrangement of isotherms is somewhat unusual. A density inversion is present in the shoal water.

Further cruises were not made until October 20–29, when the conditions of high salinity persisted although the water had undergone considerable cooling.

By December 3 (Figure 4*h*) cooling had continued through the profile and salinities continued high.

Transparency

Extinction coefficients at three stations are graphed in Figure 5. The minimum value was K=0.10, offshore, and the maximum value was K=0.45, shoal. There is no apparent correlation between transparency and stream flow or salinity, possibly because sampling was not sufficiently detailed. The data do not reflect the great decrease in turbidity that is found in Alligator Harbor in winter. In 1953, K was 3.4 in summer and 0.4 in winter in Alligator Harbor (Olson, 1955).

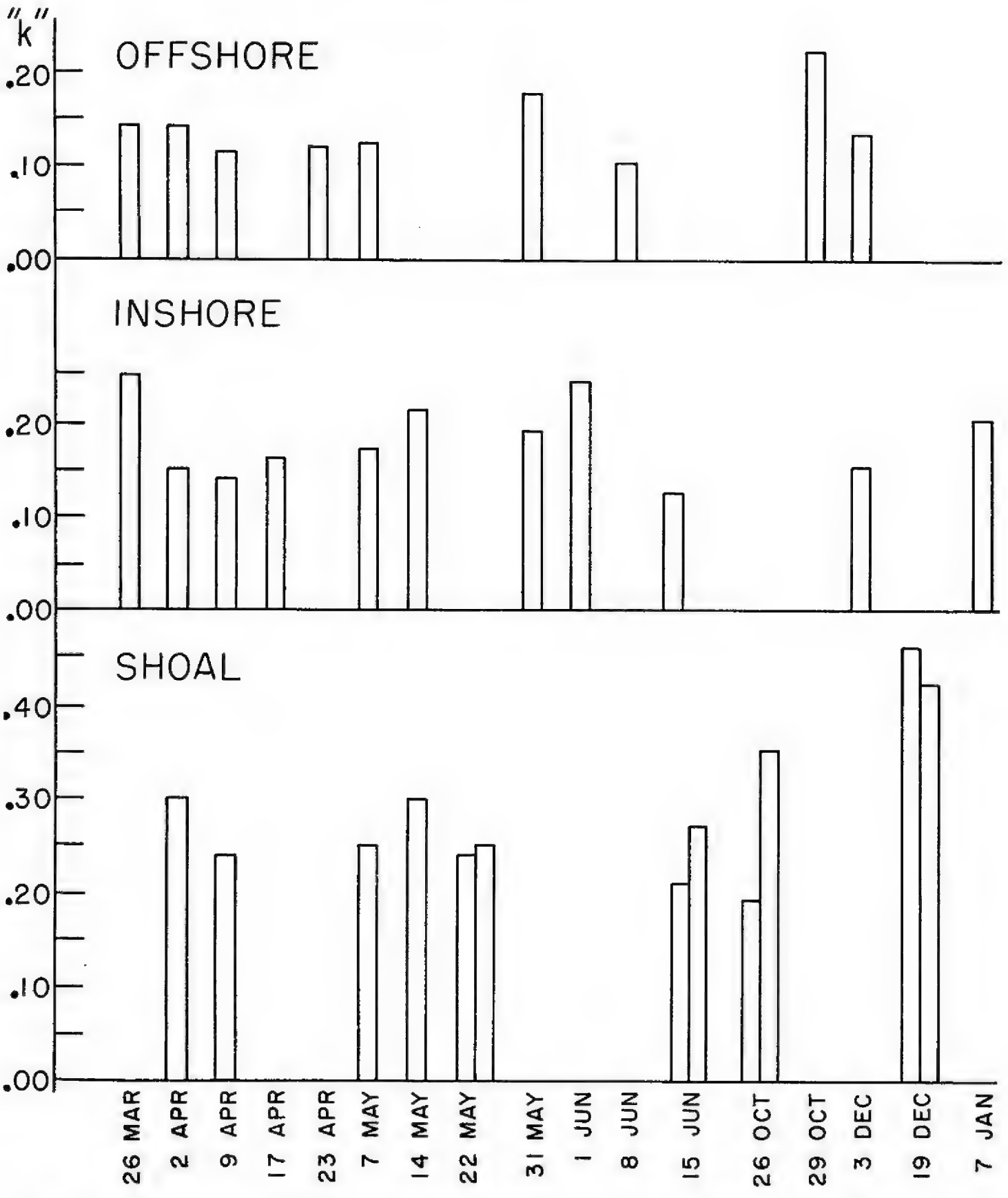

Fig. 5. Transparency of water at three stations in Apalachee Bay. Extinction coefficient "K" $= \frac{2.303}{R_{10}}$ where R_{10} is the depth at which ten per cent of the surface illumination occurs.

Clear water is found close to the coast west of Cape San Blas. At Panama City, Florida, extinction coefficients were found to vary in the range of 0.11–0.21, one-half mile from shore.

Measurements made with a submarine photometer in Apalachee Bay revealed turbidity stratification at nearly all stations. During periods of high river flow there was usually a shallow, warm, turbid layer in the upper 10 feet, and a very shallow turbid layer on the bottom.

Discussion of Water Masses

Two kinds of water, coastal and gulf, are distinguishable within 30 miles of shore. No really sharp boundary can be found most of the time. For the most part we must content ourselves with arbitrarily selecting a temperature range of 15–25°C and salinity range of 35 ppt or less, as characteristic of coastal water and a temperature range of 16–20°C and a salinity range of 35 ppt or more, as characteristic of Gulf surface water.

The source of high salinity water is the Gulf of Mexico proper. Patterns of salinity of the northeastern gulf are shown in Figure 6 based on data obtained by Texas A and M College. The source of fresh water is land drainage and direct rainfall. Rainfall is frequent and heavy and the Florida panhandle coast has an average annual precipitation of 58 inches. Heaviest rainfall occurs July through September when 7.5 inches fall per month compared with an average of 3.6 inches for the remainder of the year. The total precipitation in any year may differ by a factor of two (Table 1). (Florida was undergoing a severe drought in 1953–1954.) The other source of fresh water is stream flow. There are many rivers flowing into the northeastern gulf: the Apalachicola, Ochlockonee, St. Marks, Steinhatchee, Suwanee, and Withlacoochee. Stream flow records (unpublished, U.S. Geological Survey) for twenty-two rivers located between Tampa Bay and Cape San Blas were analysed. These data were graphed together with local salinity variations.

The flow rates of the Apalachicola, Suwanee, and Ochlockonee rivers are depicted in Figure 2. A comparison demonstrates the complete dominance of the Apalachicola River flow on the salinity distribution south of Alligator Harbor. The salinities of 36.0 to 36.5 ppt, found from 5 to 25 miles offshore, indicate the presence of gulf water rather than coastal water on much of the continental shelf in this region. This is in contrast to the low surface salinities of 30.46 to 33.73 ppt reported by Chew (1955) in the north-

TABLE 1

Precipitation anomalies for 1951 and 1954*

Location	June		July		August		Annual	
	Departure from normal (inches)	Percent departure	Departure from normal (inches)	Percent departure	Departure from normal (inches)	Percent departure	Departure from normal (inches)	Percent departure
1951								
Apalachicola, Fla.	—0.77	13.8	.....	.....	—5.70	75.5	—4.49	57.0
Pensacola, Fla.	3.03	64.7	.....	.....	—2.74	34.2	3.08	57.8
Albany, Ga.	0.47	10.2	.....	.....	0.56	9.9	—4.85	50.3
Atlanta, Ga.	0.92	23.4	.....	.....	—3.53	75.1	1.19	47.6
Montgomery, Ala.	—0.49	12.9	.....	.....	—1.77	41.8	—12.79	51.4
1954								
Apalachicola, Fla.	1.09	22.2	1.94	26.1	—4.93	63.4	—18.36	57.0
Pensacola, Fla.	—3.77	93.5	—1.21	18.3	—6.59	87.9	—29.29	57.8

* Computed from U.S. Weather Bureau Climatological Data, National Summary.

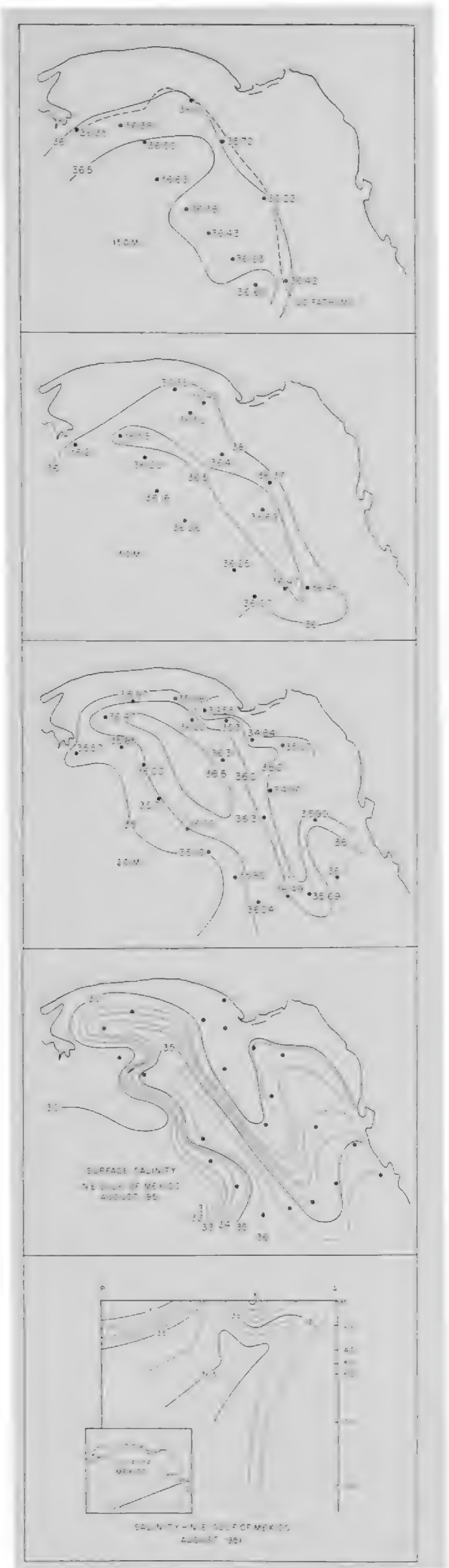

FIG. 6. Distribution of salinity in the northeastern Gulf of Mexico, August 1951. Redrawn from data in Chew (1955).

eastern gulf in later summer, 1951 (Figure 6). Salinities at 20 m were in the vicinity of 34.8 ppt. Data from the same region in 1953 showed salinities over 34.0 ppt at the surface and this was true also in 1955 (K. A. Drummond, personal communication). It is likely, then, that surface salinities rarely fall below 34 ppt in the northeastern gulf and that water of 35 ppt salinity is not uncommon at the surface inshore, especially during periods of drought.

In northern Florida the Apalachicola River is of special interest. It is the largest river in the state and drains parts of Georgia and Alabama. Although the Apalachicola is largely responsible for salinity changes off Alligator Harbor, its influence may be noted in salinity patterns at times 160 miles to the south in the gulf (Figure 6).

Ingle and Dawson (1953) and Dawson (1955) investigated Apalachicola Bay as an oyster producing area and gave some information on physical features. The bay is shallow, averaging five feet deep. At the center it is 10 feet and from 20 to 50 feet in the passes (inlets). Ingle and Dawson (1953) assert that water flow in the bay is wind-controlled. Ordinarily, high salinity water enters through East Pass and leaves *via* West and Indian Passes (U.S.C.G.S. Chart 1262) diluted with river water. Currents are strong and the channels well scoured. West Pass is the main channel. It appears probable that all the flow goes to the west with no wind or an east wind blowing. Under high river flow, or a strong west wind, some of the fresh water would be forced to the east. The data of Figure 2 support this contention. These conjectures are also supported by Figure 2 in Chew's (1955) paper. Low salinity water (28.95 ppt) is seen to extend westward from Cape San Blas at the surface.

Olson (1955) suggested that the salinity regime in Alligator Harbor is controlled by the incursion of Apalachee Bay and Ochlockonee River water. That this is probably not the case may be deduced from a precipitous decrease in salinity in mid-March, 1951 (Oceanographic Institute, unpublished), the salinity changes reported by Grice (1953), and the data for 1953 (Olson, 1955) ; all of which find a reflection in Apalachicola River flow data and in the data presented here for 1954. Moreover, Olson (1955, pp. 100–113, Figures 22A, 24B, 41–43, and 50–53) showed that clear, low salinity water was found at the surface in the Saint Theresa Channel with much higher salinity water at the bottom, while turbid, well-mixed water of moderate salinity entered Alligator Harbor through the Peninsula Point Channel.

It now seems fairly certain that the Apalachicola River water mixed with Gulf of Mexico water enters Alligator Harbor at the surface through the Saint Theresa Channel. Gulf of Mexico water, somewhat diluted with coastal water, comes in through the Duer Channel and enters Alligator Harbor via the bottom of the Saint Theresa Channel, while coastal water enters the harbor via the Peninsula Point Channel.

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The Use of Diatom Populations as a Measure of Water Quality in Selected Areas of Galveston and Chocolate Bay, Texas[1]

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Abstract

By use of the truncated log normal distribution. analysis has been made of the diatom populations from several areas in Chocolate and Galveston Bays, Texas. The results of these analyses were compared with the results of concurrent biological surveys. A chi-square goodness of fit test indicated the Catherwood Diatometer developed random, reproducible samples of diatoms. The drastic change in the shape of the diatom curve in polluted environments was shown to be correlated with a similar change in the species diversity of the flora and fauna of the biological survey. The structure of the diatom flora was the same as that previously found in Chesapeake Bay, Maryland, under similar ecological and chemical conditions.

Introduction

The Catherwood Diatometer has been successfully calibrated (Patrick, Hohn, and Wallace, 1954) for use in fresh water as a means of measuring the relative "health" of different areas of a river. This instrument collects a random, representative sample of the diatom flora growing in a river that can be analyzed and graphically represented as a truncated log normal distribution as set forth by Preston (1948) and Robert Singleton as published by A. Hald (1949). Similar studies have been carried out in the brackish water areas of Chesapeake Bay in the vicinity of Baltimore, Maryland and the Lewes-Rehoboth Canal in the vicinity of Lewes, Delaware (Academy of Natural Sciences of Philadelphia, 1954). Relationships between "healthy" and polluted areas similar to those obtained in the fresh water comparisons were shown to exist in brackish water. Further study of these relationships in brackish water was carried out in the vicinity of Galveston and Chocolate Bay, Texas during the summer of 1954. This paper is a summary of these results including comparisons with those from Chesapeake Bay and the Lewes-Rehoboth Canal.

The author wishes to thank Dr. Ruth Patrick, Curator of Limnology at the Academy of Natural Sciences of Philadelphia for her advice throughout the study. The author also wishes to acknowledge the help of the staff of the Regional Office of the Texas State Board of Health for aid in selecting the stations; Dr. W. A. Quebedeaux of the Stream and Air Pollution Division of the Harris County Health Unit for his aid in selecting the stations in Chocolate Bay and the Houston Ship Channel; Dr. T. H. Pulley, then of the University of Houston, for his aid in collecting the stations in Chocolate Bay and Mustang

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Bayou; and Mr. R. P. Hofsteter of the Texas Game and Fish Commission for his aid in locating the station in Galveston Bay.

Selection of Stations

In order to select suitable areas for study, a review was made of available chemical and biological data of the Stream and Air Pollution Division of the Harris County Health Unit. The areas were classified on the basis of these data and the species diversity found on the preliminary field studies at various points in the Houston Ship Channel, Galveston Bay, and Chocolate Bay to further pinpoint suitable study areas. The following stations were selected:

Station 1. In the vicinity of Red Flasher Beacon 70, 2 and ½ miles up the Houston Ship Channel from the San Jacinto monument.

Station 2. Galveston Bay in the vicinity of Red Beacon 66, at the southern tip of Atkinson Island, and approximately 1 and ½ miles southeast of Morgan Point.

Station 3. In Mustang Bayou approximately 200 yards from its mouth where it enters Chocolate Bay.

Station 4. Several small islands in the vicinity of red Nun Buoy 22 in Chocolate Bay, approximately 1 and ½ miles west of Horse Grove Point.

Methods

The biological survey was carried out by the survey crew of the Academy of Natural Sciences of Philadelphia as described by Patrick (1949). Since no base line of comparison had been established for brackish water conditions, histograms were not constructed for the various stations. A chart was prepared (Table 1) showing the diversity of the flora and fauna at each location. These groups were then totalled and used as a basis for comparing the total relative species diversity which has been used as a measure of the relative "health" of an area (Patrick, 1949). A station that is able to support a well-balanced, highly diversified flora and fauna is considered to be "healthy." An area that supports unbalanced populations of reduced species diversity is classified either as "semi-healthy", "polluted", or "very polluted", depending on the amount of this species reduction and the skewedness of the population. For a detailed description of the methods and criteria used in stream classification see Patrick (1949).

TABLE 1

Species numbers of the Flora and Fauna taken on biological survey, July 27–30, 1954

Organisms	Stations			
	1	2	3	4
Blue-green algae	4	2	5	7
Green and red algae	2	3	3	4
Diatoms	10	22	62	51
Fish	0	15	26	26
Protozoa	8	29	48	68
Invertebrates				
Foragers	0	8	9	5
Burrowers	0	2	6	0
Sessile forms	0	2	4	4
Totals	24	83	163	165

Low species diversity may occur in any naturally occurring extreme or special circumstance but the addition of toxic material to that circumstance will further reduce the species diversity. The comparison of the flora and fauna from two habitats that are ecologically similar will show essentially the same species diversity unless disturbed or upset by the presence of some outside force such as a toxic waste.

No attempt was made to collect all plants and animals in a given area, but emphasis was placed on securing those species that were well-established together with notes on their relative abundance and distribution within the area of study.

Diatometers were installed at each station two weeks prior to the biological survey. Slides were removed from the diatometers at the time the survey collecting was carried out. Studies in Chesapeake Bay, as well as in fresh water rivers, have shown that exposure of slides for two weeks gives an adequate sample of the diatom population for statistical analysis. The diatoms were preserved, cleaned, mounted, and the populations analyzed in the same manner as those described by Patrick *et al.* (1954). All biological collections, as well as the diatometer material, have been deposited in the various herbaria of the Academy of Natural Sciences of Philadelphia.

A complete listing of all species used in constructing Table 1 and the truncated log normal curves (Figures 1 and 2) can be had by consulting the A.P.I. Report of the Academy for 1955 (Acad. Nat. Sci. Phila. 1955). These slides have been deposited in the general collection of the diatom herbarium under numbers 8108–8111 inclusive.

Results and Discussions

On the basis that the diversity of the flora and fauna can be used to classify the "health" of a body of water, the four stations used in this study were evaluated from the survey data.

The results of the survey studies (Table 1) show a very striking difference between the two stations in the Chocolate Bay area and those in the upper portion of Galveston Bay.

The species diversity of the Chocolate Bay and the Mustang Bayou stations was very similar. There was a well-rounded population in each major group with the two stations having a total species diversity of 163 and 165, respectively. These results, together with the available chemical data, indicate that these two stations would be classified as "healthy" and may be referred to as natural brackish water areas. The only major difference between the two stations was that Chocolate Bay represented an open bay environment while Mustang Bayou represented a protected estuary, river type of environment. Although the kinds of species were somewhat different at the two stations, the total species diversity was quite similar. These findings are in agreement with results obtained in surveys of natural streams with water of good quality.

To determine if the diatom populations collected on glass slides gave a similar measure, a two-week exposure slide was analyzed from a diatometer at each station. The resulting data are given in Table 2. It can be seen from the observed species, species in the mode, and the theoretical universe, that the two populations are very similar. A Chi-square test gave a highly significant probability value of >0.05 showing the two samples were drawn from populations with the same theoretical frequencies. A Chi-square goodness of fit test of the theoretical truncated log normal distribution to the observed data also gave a P value of >0.05 providing a reasonable fit to the data.

TABLE 2

Summary of data from Catherwood diatometers for four survey stations, July, 1954

	Stations			
	1	2	3	4
Dispersion factor	.258	.209	.226	.198
Modal interval	1.3	1.8	1.9	1.8
Species inmode	6.3	9.0	21.1	18.8
Species observed	36	60	139	130
Theoretical universe	43.2	76.2	165.2	168.1
Total specimens counted	26,600	7,689	23,918	16,856
Specimens used in construction of curve	600	2,689	9,572	5,936

Using the results of the biological survey and diatom population analyses from these two stations as a base line, similar studies were conducted in the Houston Ship Channel and the upper portion of Galveston Bay, areas known to be severely damaged by pollution.

The data in Table 1 shows that the flora and fauna at Station 1 on the Houston Ship Channel were very restricted in their species diversity. The severity of the pollution is most strikingly illustrated by the absence of fish and invertebrates as well as the reduced diversity of the other groups. A total of 163 species of plants and animals were observed in Mustang Bayou, an ecologically similar area, while only 24 species were observed in the Houston Ship Channel. The drastically reduced species diversity together with the adverse chemical data (Acad. Nat. Sci. Phila., 1955 and Chambers, 1959) indicate that this area would be classified as polluted.

An analysis of the diatom flora secured from diatometer slides from this station also showed a very much altered pattern. As compared to the "healthy" Mustang Bayou, this station showed drastic reductions (Table 2) in observed species from 139 to 36, species in the mode from 21.1 to 6.3 and in the theoretical universe from 165.2 to 43.2. There was also a drastic shift in population balance as indicated by the one species that made up 97 per cent of the total specimens observed.

The truncated log normal curves (Figure 1) show an apparently drastic difference between these two populations. A Chi-square test for goodness of fit of the theoretical to the observed data gave a probability value of >0.05 as was the case in Chocolate Bay.

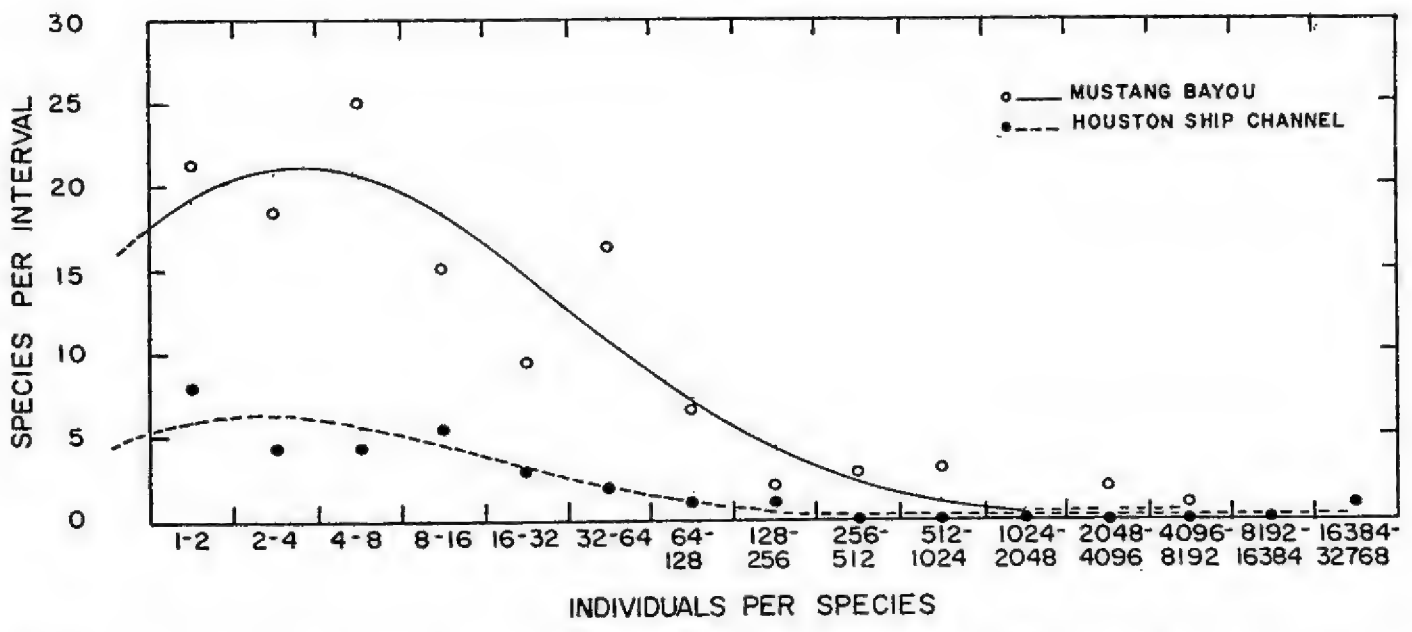

FIG. 1. Truncated log normal curves for the diatom populations of Mustang Bayou and Houston Ship Channel, Texas.

However, a Chi-square test gave a probability value of <0.05 (<0.000000) indicating a highly significant difference between the two populations.

The flora and fauna from the station in upper Galveston Bay showed a somewhat greater diversity than that found in the Houston Ship Channel. This diversity was, however, still considerably lower (83 species) than the comparable healthy area of Chocolate Bay (165 species). The conditions for survival of these organisms were undoubtedly somewhat improved due to the greater dilution of the bay water and reduction in relative toxicity. This station did, however, have such a reduced species diversity that it must also be classed as polluted.

The diatom flora, as at Station 1, showed an altered pattern, although there was apparently a slight improvement over Station 1. This diatom pattern when compared to Chocolate Bay was greatly altered. There was a reduction in observed species from 130 to 60, species in the mode from 18.8 to 9.0, and the theoretical universe from 165.2 to 76.2. The Chi-square test for goodness of fit of theoretical to observed data showed there was no significant difference between the data at the >0.05 level. There was, however, a highly significant difference at the <0.05 level ($<.000015$) between the diatom population in Galveston Bay and that found in Chocolate Bay. These two samples could be assumed not to have come from populations having the same theoretical frequencies. This is graphically represented in Figure 2.

On the basis of the foregoing data it is apparent that the log normal curve is a satisfactory method for plotting diatom populations as collected on glass slides by use of the Catherwood Diatometer. This method will provide a purely objective means, using the Chi-square test, for comparing the diatom populations from different areas of the same bay or similar bays. These data can be correlated with biological survey results to provide an accurate though rather simple method for judging water quality.

It is interesting to note the similarity of the structure of the diatom flora from "healthy" stations in estuarine areas of Texas, Delaware, and Maryland (Table 3). The results from these four "healthy" stations are quite similar and show no significant variation. This similarity is also evident when one compares the diatometer data (Table 4) from polluted estuarine areas from Texas and Maryland.

The great similarity of these results indicate that the structure of the diatom flora is

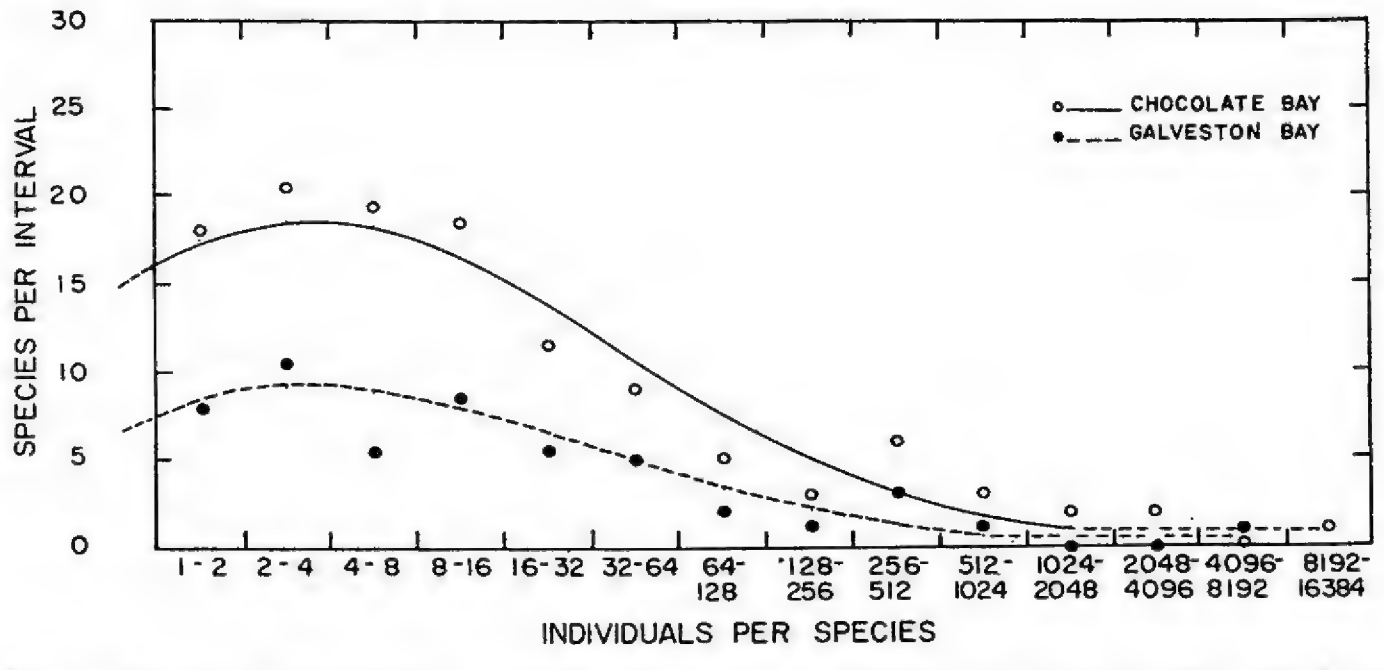

FIG. 2. Truncated log normal curves for the diatom populations of Chocolate Bay and Upper Galveston Bay, Texas.

TABLE 3

Comparison of diatometer results from healthy estuarine stations in Texas, Maryland, and Delaware

	Bay stations		Canal stations	
	Nabbs Creek, Maryland	Chocolate Bay, Texas	L.-R. Canal, Delaware	Mustang Bayou, Texas
Species in mode	18.7	18.8	20–22	21
Observed species	125	130	136–144	139
Theoretical universe	161	168	182–197	165
Specimens in body of curve	8,103	9,572	8,730–8,691	5,936

TABLE 4

Comparison of diatometer results from polluted estuarine areas in Texas and Maryland

	Curtis Bay, Maryland	Head of Galveston Bay, Texas
Species in mode	7	9
Observed species	41	60
Theoretical universe	55	76
Specimens in body of curve	1,942	2,689

quite similar in these two areas and that changes in diatom population structure as manifested by pollution are clearly demonstrable by use of the Catherwood Diatometer.

Conclusions

The results of this study clearly illustrate the feasibility of using random diatom populations as collected on glass slides in a Catherwood Diatometer as a measure of water quality in estuarine areas. There is evidently a direct relationship between the changes in structure of the diatom flora and the effect of pollution. In a "healthy" area there is a diverse and well-balanced diatom flora but an area effected by pollution supports a meager and unbalanced diatom population. Although considerably more study of this type must be undertaken before exact relationships can be established, the results of this study can serve as a starting point.

The Chi-square test can be used as an objective means of comparing diatom populations to test the probability that two samples were secured from diatom populations that had the same theoretical frequencies. These results should be correlated with biological survey results to determine the level of significance that show definite changes in water quality.

These preliminary results also indicate that the structure of the diatom flora is similar in estuarine areas of Texas, Maryland, and Delaware. The effects of pollution as manifested by changes in diatom population structure are very much the same in both geographical areas.

The Catherwood Diatometer can provide an accurate yet relatively simple method for monitoring the diatom flora in bay areas on a yearly basis and hence reflect changes in water quality through time.

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An Ecological Survey of the Houston Ship Channel and Adjacent Bays

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Abstract

An ecological survey of the Houston Ship Channel and adjacent bays was initiated in the summer of 1957 with data collected at frequent regular intervals. This report includes the comparison of data on temperature, chlorinity, dissolved oxygen, and related quantities with data on fish, shrimp, and crabs caught in trawls. Data are also given on currents, bottom cores, and organic content of sediments.

In the ship channel a dissolved oxygen gradient existed from a low dissolved oxygen concentration in the upper channel to near normal concentrations at the lower boundary of the survey area. The dissolved oxygen in the ship channel below the mouth of the San Jacinto River is greatly influenced by the flow rate of the river which is, in turn, largely controlled by rainfall.

Studies of bottom samples demonstrated that extensive silting has occurred in the ship channel and bays. Low dissolved oxygen, hydrogen sulfide production, and high organic content of the mud in the channel, all indicative of organic pollution, prevent the establishment of a normal bottom fauna.

In the bays adjacent to the channel the dissolved oxygen concentration is independent of the flow rate of the San Jacinto River, being dependent on phytoplankton production of oxygen and, at certain seasons of the year, fluctuating widely in a diurnal cycle. The concentration may range from supersaturation to extremely low concentrations in a relatively short period.

A small temperature gradient was found in the ship channel, two or three degrees higher in the upper channel than in the lower part of the survey area. When dissolved oxygen (D.O.) level is sufficient, a large and diverse population of fishes exists throughout the bays in the survey area and for a considerable distance above the Humble Oil & Refining Company's outfall.

The species composition of this population varies with the season, with predominantly marine fishes during the summer when the salinity is high and predominantly fresh water fishes in the winter when the salinity is lowered. Both the number of species and diversity of fishes present decreased up the channel.

The Humble Oil & Refining Company discharges approximately 15 million gallons of refinery waste water into the lower end of the Houston Ship Channel each day. No lowering of the dissolved oxygen concentration of the ship channel attributable to Humble's effluent was found and no effect was found to be exerted on the fish populations of the ship channel and adjacent bays by Humble's operations.

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Introduction

An ecological survey of the Houston Ship Channel and adjacent bays in the vicinity of Humble Oil & Refining Company's Baytown refinery was begun in the summer of 1957. Humble Oil & Refining Company discharges about 15 million gallons of refinery waste water per day into the lower end of the Houston Ship Channel near Baytown. Determination of what effect, if any, this discharge has on the ship channel and adjacent bays was the primary motivation of the study. Hydrographic, chemical, and biological data were collected at frequent, regular intervals and a study of the bottom composition and fauna was carried out.

The ecology of this area has not been studied intensively in the past. During several years prior to the survey, a number of chemical determinations, particularly of dissolved oxygen content, had been made at irregular intervals in these waters. In 1955 a study was conducted by Humble in which a number of sampling stations were utilized. The results of these studies were not reported in the literature. As a part of the Catherwood Diatometer Survey in the Gulf Coast area, Patrick (1955) made a study of the Houston Ship Channel and Trinity Bay (Hohn, 1959). Reid (1955, 1955a, and 1956) studied the ecology of East Bay, an embayment off Galveston Bay just south of Trinity Bay. Since ecological studies on gulf estuaries are not numerous, Humble Oil & Refining Compay made these data available for publication as a contribution to the knowledge of estuarine ecology. This report presents the data, observations, and conclusions of the

first year of the study. The observations have been continued in the hope of obtaining a more complete understanding of the various facets of the environment.

Acknowledgment

We are grateful to the Humble Oil & Refining Company for permission to publish the results of this survey. The authors sincerely express their appreciation to Mr. G. F. Viereck for his help in obtaining the field data. The authors are indebted to Dr. Gordon Gunter for the identification of juvenile croakers to species and for kindly giving advice on the taxonomy involved.

Description of the Area

The Houston Ship Channel, above Galveston Bay, is an artificial stream created by deepening and straightening Buffalo Bayou and maintained by periodic dredging. Numerous streams and bays empty into it and receive a tidal exchange, the extent of which depends on the distance up the channel from Galveston Bay, the stage of the tidal cycle, and, especially, meteorological conditions (see maps, Figures 1, 2 and 3). It serves as the sole means of access for ocean-going vessels to the Port of Houston, one of the world's busiest ports. Numerous industries, including chemical and petrochemical plants, oil refineries, a paper mill, and a steel mill line the ship channel and discharge their effluents into it and its tributaries. In addition, the City of Houston and towns and communities along the banks, totalling almost a million people, discharge sanitary sewage into these streams after varying degrees of treatment.

Thus, the upper part of the Houston Ship Channel receives a substantial quantity of waste material and its ability to sustain fish life is, at best, a delicate balance between conditions just barely marginal for typical aquatic life and a biological desert. The upper limit at which aerobic aquatic life is maintaned moves up and down the channel, depending upon the relative amounts of discharged material and the meteorological and hydrographic conditions. Patrick (1955), based on data obtained from the Harris County Health Unit, writes, "the effects of these wastes are very severe as far down the

Fig. 1. Location of the survey area on the Texas coast.

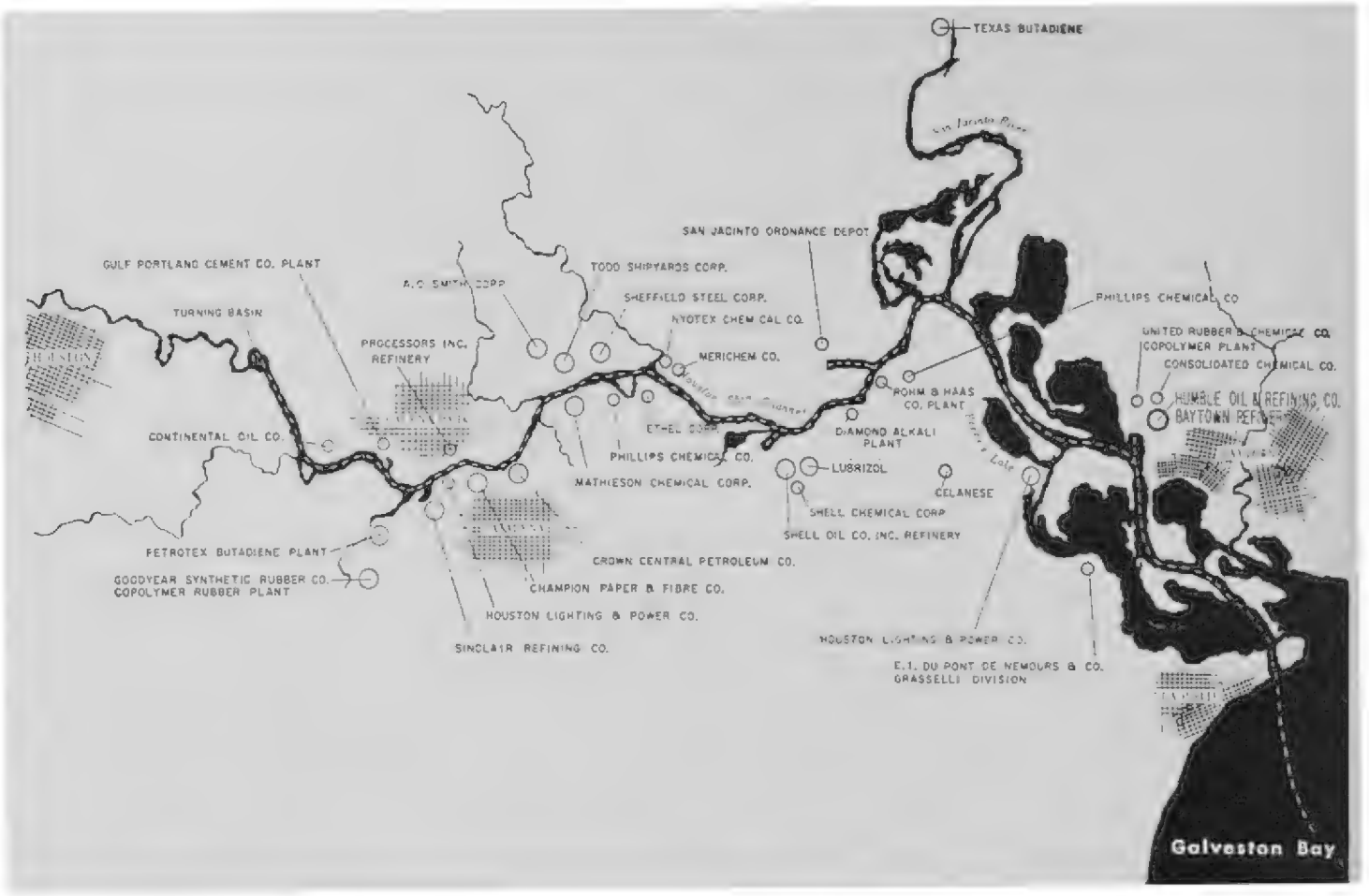


FIG. 2. Principal plants in Houston Ship Channel industrial area.

Channel as the Lynchburg Ferry" (mouth of San Jacinto River). "At this point the first signs of dissolved oxygen are evident and the BOD load is reduced."

The flow of the San Jacinto River has been decreased by the construction of dams on the San Jacinto River and almost ceases during periods of low rainfall. The fresh water from the river and the shallow bays add to the recuperative powers of the water coming down the ship channel, so that there is water of generally higher quality in the channel downstream at Baytown as compared with the channel above the San Jacinto River.

The area routinely studied in the survey extends from Buoy 143, approximately seven miles above Humble's waste outfall to the tunnel crossing approximately two miles below the outfall, and includes stations in the San Jacinto River, Burnett Bay, Crystal Lake, and Scott Bay. A map of the survey area and the location of the sampling stations are shown in Figure 3.

MATERIALS AND METHODS

Dissolved oxygen determinations were routinely made twice each week at each station by means of a portable polarographic analyzer developed by Tyler and Karchmer (1959). This device has been found to be rugged, simple to use, and produces immediate, accurate results. On one occasion the dissolved oxygen content was determined at frequent intervals at one bay location over a fifty-hour period. Samples for dissolved oxygen determinations were collected in pint bottles at depths of 12 to 16 inches and were analyzed immediately using the portable analyzer. Oxygen was not measured at greater depth where lower values might have been found.

The accurate determination of dissolved oxygen by the polarographic method requires that the temperature of the sample be determined while the polarograph reading is being made. Thus, the temperature of each sample used for dissolved oxygen determinations was recorded during the course of the survey. Since the sample is run immediately after

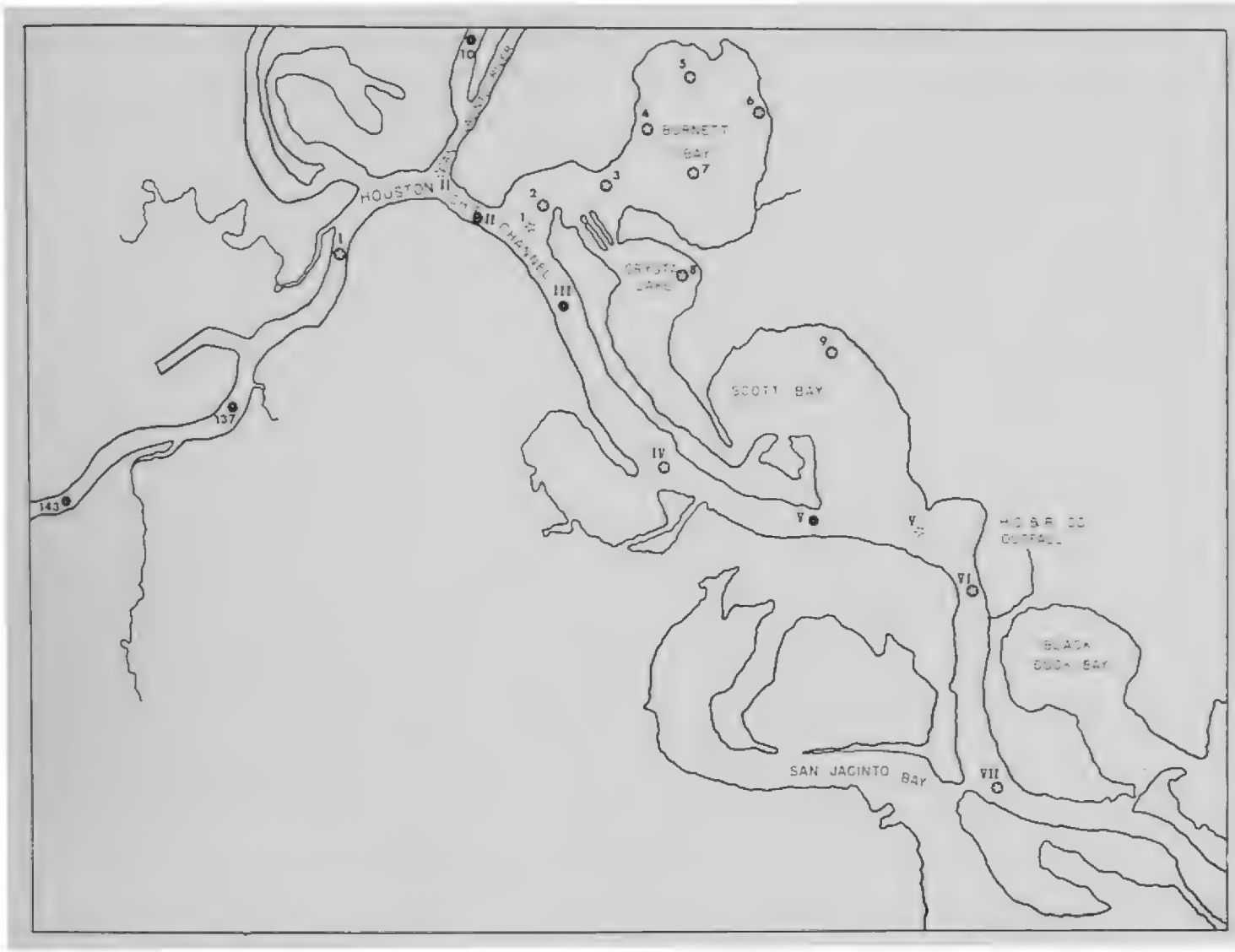


FIG. 3. Sampling Stations. Stars indicate stations sampled on September 1, 1957; black circles indicate stations after January 30, 1958.

being taken, the measured temperature represents very closely the temperature of the channel or bay water 12 to 16 inches below the surface, and is so considered in a later section for the purpose of discussing temperature variations in the survey area.

Determinations of the chloride content of water samples were made routinely at one-week intervals. The water samples were collected at a depth of approximately four inches at certain stations and analyzed by the Volhard method. Measurements of specific conductance and temperature at various depths were taken by the use of a model RB1881 portable Solu bridge and a conductivity cell with 50 feet of connecting cable.

Currents in the Houston Ship Channel and the bays were studied by several methods. Chlorinities were of value in determining current patterns. A Price Pattern Current Meter was used on two occasions for sub-surface current velocity determinations, but was found to be generally unsatisfactory for work in the bays, and frequently in the Channel, because the current velocity was often too low to activate the meter, and in any case, the direction of the current was not indicated. Surface current determinations of the San Jacinto River were made at weekly intervals at Station 10 and at other locations on certain occasions by means of a one-foot by two-foot current cross.

Tidal data were obtained from the Humble Dock Department, where records of the reading of a tide gauge have been maintained for a number of years. Wind direction and velocity records, also obtained from the Dock Department, are of considerable importance in understanding the hydrography of the area. A tide staff was set up in the entrance to Burnett Bay so that the tidal height at this location could be correlated with that at the Humble Dock. Rainfall data were obtained from rain gauge records of the

Humble Refinery. Elevation data on Lake Houston were obtained from the San Jacinto River Authority.

Bottom studies were made by two methods. In the first method, developed by Dr. J. G. Mackin, cores were collected in Pyrex glass tubes in a coring device developed at the Texas A & M Research Foundation Marine Laboratory, Grand Island, Louisiana. This device is provided with a vacuum arrangement to retain the core when removing the device from the water. The cores were transported to the Texas A & M Research Foundation Marine Laboratory, cleaned, and examined under a strong light. A sketch was made of each core. Each core was then forced by air pressure from the tube into a wooden trough. A one-inch section from each stratum was removed, emulsified in tap water and poured through a series of U.S. standard sieves ranging from 1/10th to 1/200th of an inch in mesh size. A particle size distribution of each section was thus obtained. The sieves were then examined with a stereoscopic microscope.

In the second method, an Ekman dredge was used. With this dredge it was possible to obtain samples in deeper water than with the coring device, but only the top layer of the bottom sediments could be sampled. Samples taken with the Ekman dredge were sieved and studied for bottom fauna and nature of particles after a portion had been removed for chemical analysis. Analyses were made for organic content.

Studies of the fish and larger invertebrates were made at certain localities each week by means of a standard 10-foot otter trawl (1⅜ inches × #9 × #15) with 12 inch × 24 inch trawl boards. Specimens were identified and counted in the field and the data were tabulated along with hydrographic and meteorological data on a collection card. Sampling methods were standardized to the extent that trawls were made at the same location and at the same towing speed each week, initially as follows: (1) Station 2 to Station 3; (2) Station 4 to Station 5; (3) Station 6 to Station 7; (4) around Station 8; and (5) in a circle around Station 9. The trawl between Station 2 and Station 3 was discontinued on January 30, 1957, and a trawl beginning at Station III and continuing up the channel for 700 yards was initiated. In March, trawls starting at Station 137 and at Station VII and, in each case, continuing for 700 yards up the channel were begun.

Data on physical and chemical conditions and the fish and larger invertebrates collected in the otter trawls were first transferred to a specially prepared form for key punching. The data punched on International Business Machine Company (IBM) cards (No. 804118) were then transferred to magnetic tape. A program for the IBM 705 calculator was set up to print out the conditions at which each species was collected so that the relationships of various physical and chemical conditions and the organisms collected could be more readily analyzed. A few species with associated environmental factors were treated on a more numerical basis with the aid of the IBM run.

The data collected on species of particular interest or those on which sufficient data were available were treated in the following ways: the catch per trawl for a species at each station was tabulated by station, date, chlorinity, D.O., and temperature intervals. The intervals used were 500 ppm, 0.5 ppm, and 5° F.

Hydrography

Chlorinity

Chlorinities in this study were routinely determined at one-week intervals at some of the survey stations. These data reported as chlorinities may not be used to calculate

salinities because considerable sodium chloride and other inorganic compounds are believed to enter the Houston Ship Channel, thus the normal salt ratio of sea water is upset. The samples were collected near the surface where there is a tendency for fresh water to ride on top of the salt water tidal wedge. All chlorinities obtained in the study are listed in Tables 1 and 2 by station and by date.

Data from typical stations have been selected to show the seasonal variation in chlorinity in the survey area: Station 137 (Figure 4) is typical in salinity of the ship channel above the San Jacinto River; Station 10 (Figure 4) shows the influence of the San Jacinto River; Station 7 (Figure 5) is typical of the bays; Station VII (Figure 5) is the most seaward station to be discussed.

Fluctuations in chlorinities occur in a cyclic fashion and in a seasonal pattern because of variation in the amounts of rainfall and evaporation. Tidal differences, both meteorological and astronomical, influence the chlorinity in a seasonal pattern. Predominant winter winds in this area are from the north causing, during a considerable part of the winter, the tidal exchange to be lessened at the same time that the greatest dilution by run-off and San Jacinto River discharge occurs. In the summer the predominant winds are from the south, intensifying the effect of tides. The tide in the Gulf of Mexico is largely diurnal with a single high and low daily tide, and in yearly fluctuation creates a higher sea level during the second half of the year than in the first half (Marmer, 1954.)

TABLE 1

Chlorinity in ppt at channel stations from October, 1957, through July, 1958

	October, 1957					November, 1957				December, 1957			
Station	3	10	16	17	31	7	14	21	27	5	12	19	26
VII	6.3	7.3	....	0.4	....	....	2.0	2.8	0.5	4.0	7.3	....	6.9
V	....	6.6	....	0.3	3.7	....	1.3	2.4	0.2	3.6	6.6	7.1	6.4
III	....	....	....	....	....	....	....	....	....	....	....	....	....
II	....	....	....	....	....	....	....	....	....	0.9	3.5	....	3.6
I	5.6	6.9	0.3	0.1	4.2	4.6	2.4	2.0	0.1	3.6	5.8	7.2	8.9
B 137	....	....	....	....	....	....	....	....	....	....	....	....	....
B 143	....	....	....	....	....	....	....	....	....	....	....	....	....
10	5.5	3.3	0.3	0.1	0.5	3.7	0.1	0.2	*	0.1	1.0	2.8	1.5

	January, 1958					February, 1958				March, 1958			
Station	2	9	16	23	30	6	13	20	27	13	20	21	27
VII	3.6	5.1	1.5	0.3	1.3	1.6	3.2	5.6	1.1	5.1	6.8	....	7.3
V	3.1	....	....	....	0.8	1.5	2.6	5.1	0.7	4.6	6.4	6.7	6.8
III	....	....	....	....	0.2	1.0	1.7	3.9	0.6	3.5	5.5	6.2	5.6
II	0.2	0.4	*	0.1	0.2	1.2	1.6	3.9	0.2	2.7	5.7	5.0	5.4
I	1.1	1.8	0.5	0.4	0.2	1.6	1.5	3.0	0.6	2.9	5.6	5.0	5.1
B 137	....	....	....	....	....	....	....	....	1.8	4.8	5.6	7.0	6.5
B 143	....	....	....	....	1.5	1.7	2.6	4.0	1.7	4.8	5.4	4.8	6.5
10	0.1	0.1	*	0.4	*	0.5	0.4	2.1	*	1.4	3.5	3.7	3.3

	April, 1958			May, 1958					June, 1958			July, 1958			
Station	2	10	24	2	8	15	22	28	5	12	26	2	10	17	31
VII	7.6	7.4	6.2	5.6	1.2	4.5	5.2	4.6	3.9	2.3	3.1	3.2	4.9	4.2	4.0
V	8.5	6.7	5.6	5.7	0.8	4.4	5.0	4.5	4.8	2.8	4.1	5.1	5.1	4.2	5.4
III	7.6	6.0	4.4	4.9	0.6	4.3	4.6	4.3	4.5	3.5	4.1	5.4	4.6	4.5	4.9
II	7.5	5.6	4.9	4.7	0.4	4.3	4.5	4.1	4.3	3.8	3.9	5.0	4.5	....	4.9
I	7.3	5.3	3.7	3.9	0.4	4.0	4.7	4.4	4.2	4.0	3.6	4.9	4.0	4.2	4.4
B 137	7.2	6.0	4.6	4.1	0.9	4.2	4.5	4.4	3.9	3.9	3.4	4.7	3.9	4.2	4.3
B 143	6.7	5.8	5.1	4.2	1.5	4.2	4.6	4.2	4.0	3.8	3.2	4.7	3.9	3.8	4.1
10	6.1	4.0	2.0	2.7	....	2.8	4.6	3.3	4.2	4.1	3.6	5.0	4.3	4.8	4.5

* Less than 0.1 ppt.

This entire area is characterized by extreme fluctuations in chlorinity over short periods of time, due both to flow of the San Jacinto River and to surface run-off in the ship channel and City of Houston area. We find decreases in chlorinity of as much as 6500 ppm within one week (Figure 5).

TABLE 2

Chlorinity in ppt at bay stations from October, 1957, through July, 1958

	October, 1957					November, 1957				December, 1957			
Station	3	10	16	17	31	7	14	21	27	5	12	19	26
2	5.5	6.7	1.2	0.3	2.7	5.8	1.7	2.5	*	1.1	6.0	6.2	6.3
3	5.4	6.4	1.1	0.4	2.3	4.2	1.7	2.1	*	0.9	5.8	5.9	6.3
4	5.2	6.0	3.1	1.7	2.1	3.8	2.2	1.8	0.3	0.9	2.6	5.4	6.2
5	5.1	3.7	....	1.9	2.0	....	2.4	1.7	0.4	0.9	3.1	5.2	6.0
7	5.2	6.0	2.6	1.0	2.2	....	2.2	1.8	0.3	0.9	3.0	5.7	6.2
6	5.0	6.0	3.1	1.1	2.2	....	1.8	1.7	0.2	1.0	4.2	5.4	6.2
8	5.1	6.4	2.6	1.7	2.9	....	2.3	2.0	0.2	1.5	4.1	6.0	6.1
9	5.4	6.6	3.1	1.3	3.1	....	2.5	2.0	0.1	1.5	4.6	6.4	6.9

	January, 1958					February, 1958			March, 1958		
Station	2	9	16	23	30	6	13	20	13	20	27
2	2.2	2.7	1.5	0.2	....	1.1	1.8	3.8	3.5	5.5	6.0
3	3.1	3.2	1.9	0.4	0.5	0.6	2.2	3.6	3.6	4.8	5.6
4	3.5	3.3	1.9	0.4	0.5	0.5	2.1	....	....	4.5	5.2
5	4.8	3.1	1.8	0.4	0.5	0.4	2.2	....	....	4.5	5.4
7	2.9	3.1	....	0.4	0.5	0.6	....	3.7	3.6	....	5.3
6	4.8	3.1	....	0.3	0.5	....	....	3.7	3.5	....	5.4
8	3.6	3.1	1.5	0.3	0.7	0.9	....	3.9	3.7	5.0	5.8
9	3.1	4.2	2.9	0.3	0.5	1.4	2.4	4.7	4.8	5.0	6.5

	April, 1958				May, 1958				June, 1958			July, 1958			
Station	2	10	16	24	8	15	22	28	5	12	26	2	10	17	31
2	6.8	5.9	....	4.9	....	3.3	4.5	....	4.4	3.7	3.4	....	....	4.5	4.8
3	6.2	6.5	....	4.6	....	2.4	4.4	4.0	4.4	4.1	3.7	....	4.5	4.4	4.6
4	6.2	....	....	4.9	....	2.0	3.5	....	4.2	4.2	....	4.8	4.5	4.5	....
5	6.1	....	....	5.1	....	1.7	....	....	4.1	4.3	....	4.3	4.5	4.5	....
7	6.1	6.3	5.1	5.0	2.3	1.9	....	....	....	....	3.8	4.4	4.9	4.4	4.3
6	6.0	5.9	5.1	5.1	1.9	1.8	....	....	....	....	....	3.8	4.5	4.5	4.3
8	6.8	6.8	....	5.8	....	2.0	....	....	....	3.6	3.6	....	....	4.5	4.4
9	7.4	7.8	....	6.0	2.0	2.4	....	....	....	3.5	4.0	5.5	5.1	....	4.9

* Less than 0.1 ppt.

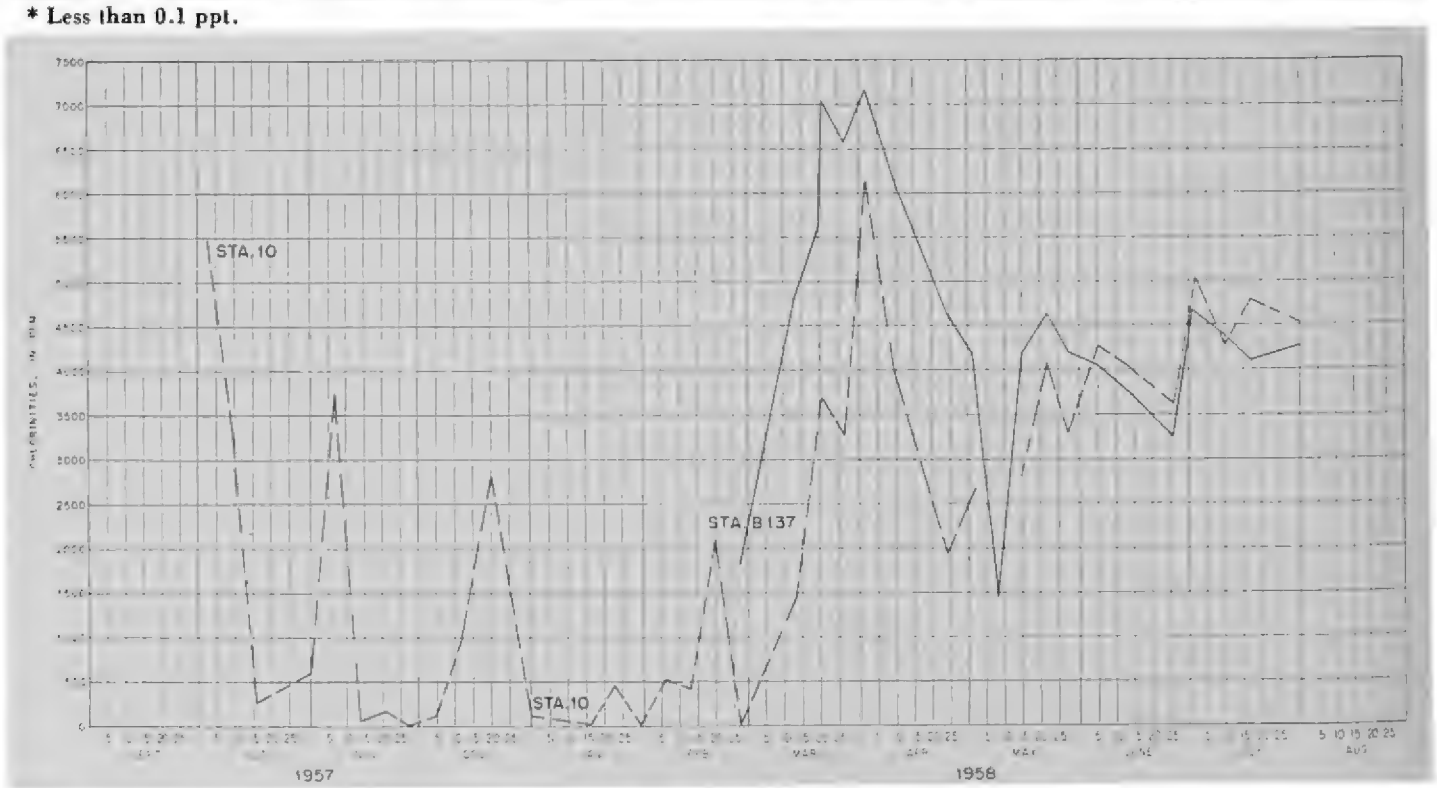


FIG. 4. Chorinities of the upper channel (Station 137) and of the San Jacinto River (Station 10).

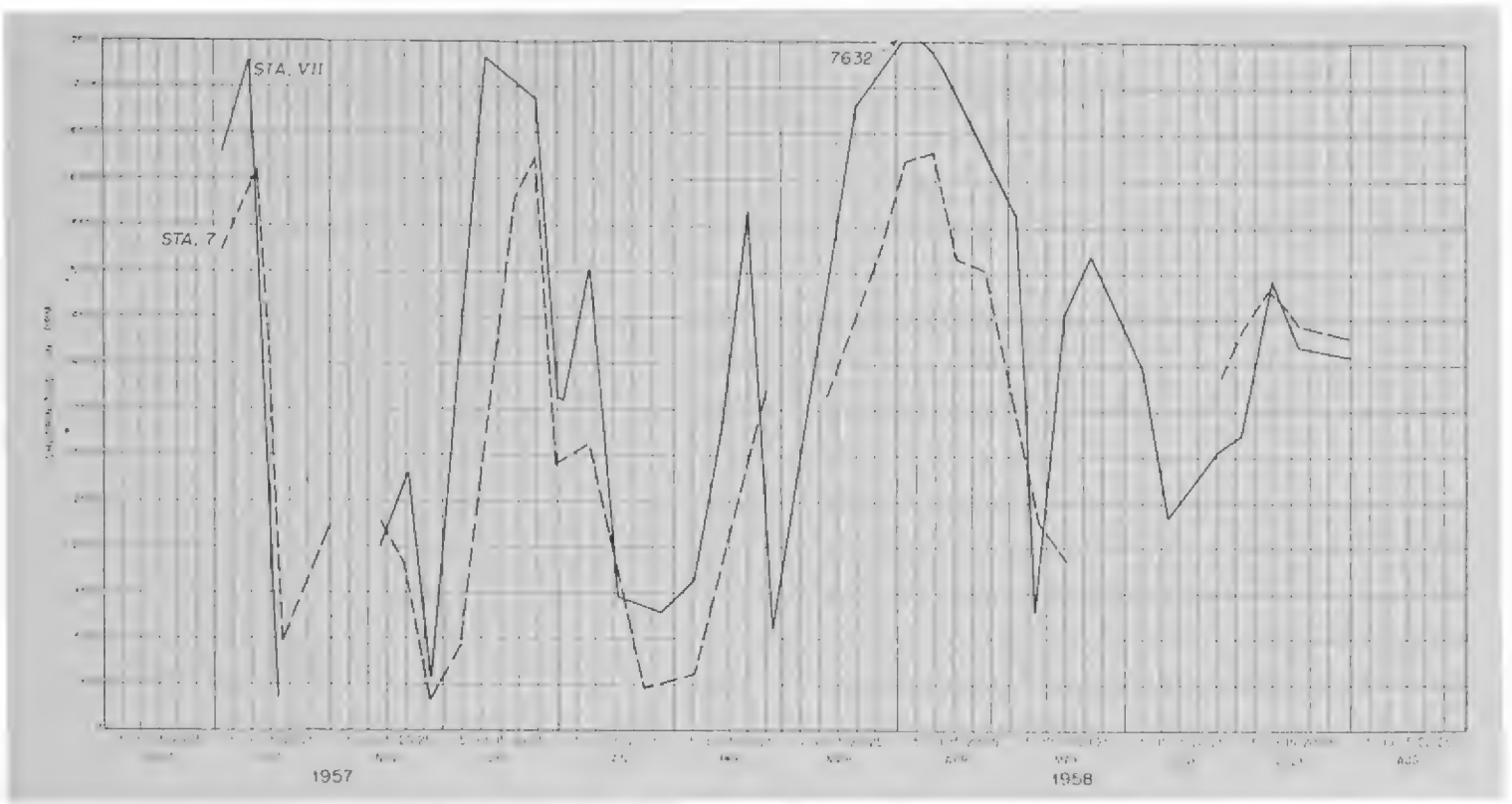


FIG. 5. Chlorinities of the lower channel (Station VII) and of Burnett Bay (Station 7).

There is usually a considerable variation in the salinity in the ship channel from the upper to lower parts of the survey area. This condition is not so pronounced in the bays; water of either high or low salinity is sometimes trapped in the bays and resists transfer for considerable periods as described in the section on seasonal changes in Burnett Bay.

TEMPERATURE

Temperatures in the survey area vary considerably from the station at the Baytown Tunnel Crossing to Station 143, occasionally by as much as 6° F. Considerable variation exists between the temperatures of the Ship Channel and the adjacent bays, and there is some seasonal variation at each station.

Typically, temperatures increase in the Houston Ship Channel from a low point at Station VII (the tunnel crossing) or Station VI to a maximum, for the area being studied, at Buoy 143. The extreme range of temperature measured during the survey period was 7° F (Figure 6) which occurred on March 20, 1958, but the trend was almost always present. It is not known what effect, if any, the gradual increases in the temperature up the ship channel have on the ecology of the area.

The same seasonal temperature trends were present throughout the survey area, but the upper ship channel was almost always a few degrees warmer than other locations. The bays, being shallow and relatively stationary, were influenced more by meteorological conditions than the ship channel or the San Jacinto River (Figures 7 and 8, and Table 5).

The routine measurements of temperature of the ship channel and bays discussed previously were made in the upper one foot of water. On April 15, 1958, and May 6, 1958, studies were made of the vertical distribution of temperature and conductivity. Although the conditions found on these two occasions are not necessarily typical they demonstrate the non-homogeneous nature of the ship channel while, at the same time, they show the homogeneous nature of the bay water. There is also a vertical gradient of conductivity indicated by the data in Figures 9 and 10.

On April 15 the temperature at Station 7 in Burnett Bay was the same at the three

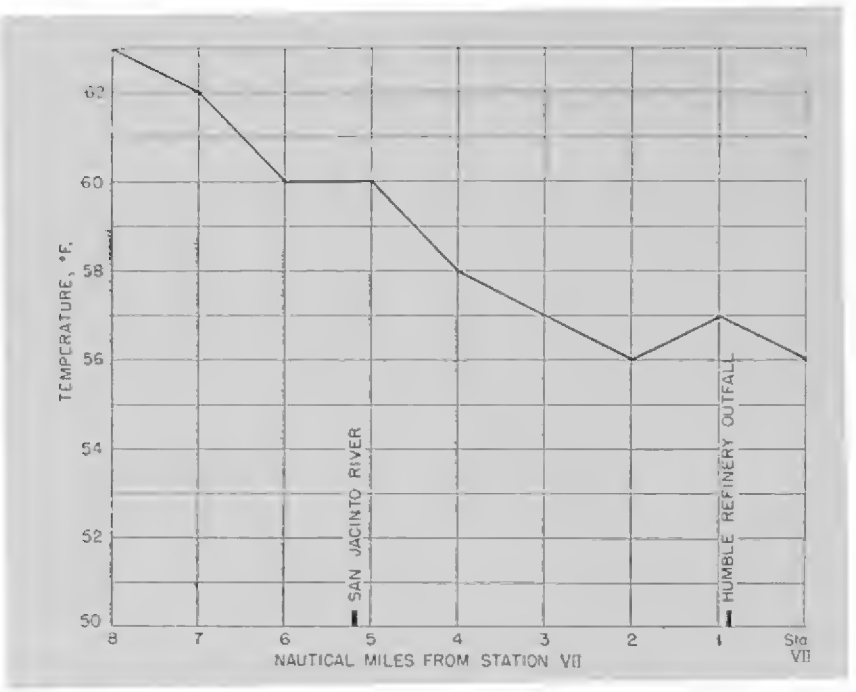


FIG. 6. Distribution of temperature in the Houston Ship Channel on March 20, 1958.

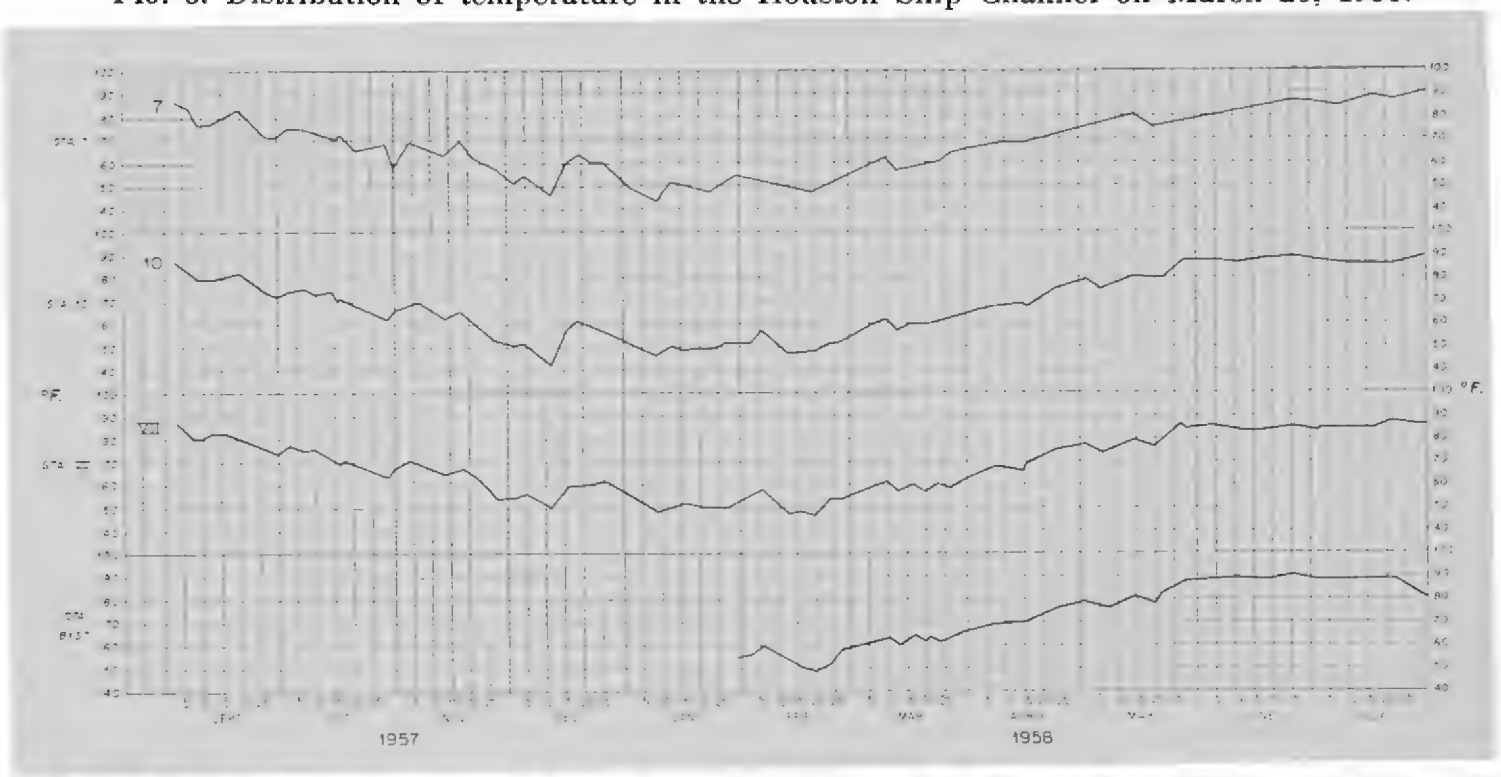


FIG. 7. Temperatures at selected channel and bay stations from September 1957 through July 1958.

depths sampled; the specific conductance was also constant, 14,000 micromhos/cm, at all depths. By contrast, temperatures were elevated from 3°F to 6°F between the surface and the second foot depth in all channel stations. After the initial elevation the temperature remained relatively constant for the remaining depths down to 30 feet. At the time the temperatures were rising, the conductance was also rising. Apparently the cooler, fresher water was flowing down the ship channel on top of a salt water wedge of warmer, more saline water.

CURRENTS

Lines drawn through the points of equal conductance in Figures 9 and 10 outline a salt water wedge which lies under the fresh water inflow. The fresh water inflow from the San Jacinto River on May 6, 1958, appeared to be lens shaped in the upper layer of the channel. The San Jacinto River on this day had a flow rate of 0.86 feet per second and a conductance of 235 to 240.

Data from a hydrographic survey conducted in January are shown in Table 3. The results of the January survey show that the San Jacinto River water, upon entering the channel, rides over the channel water and then continues downstream in the upper layer

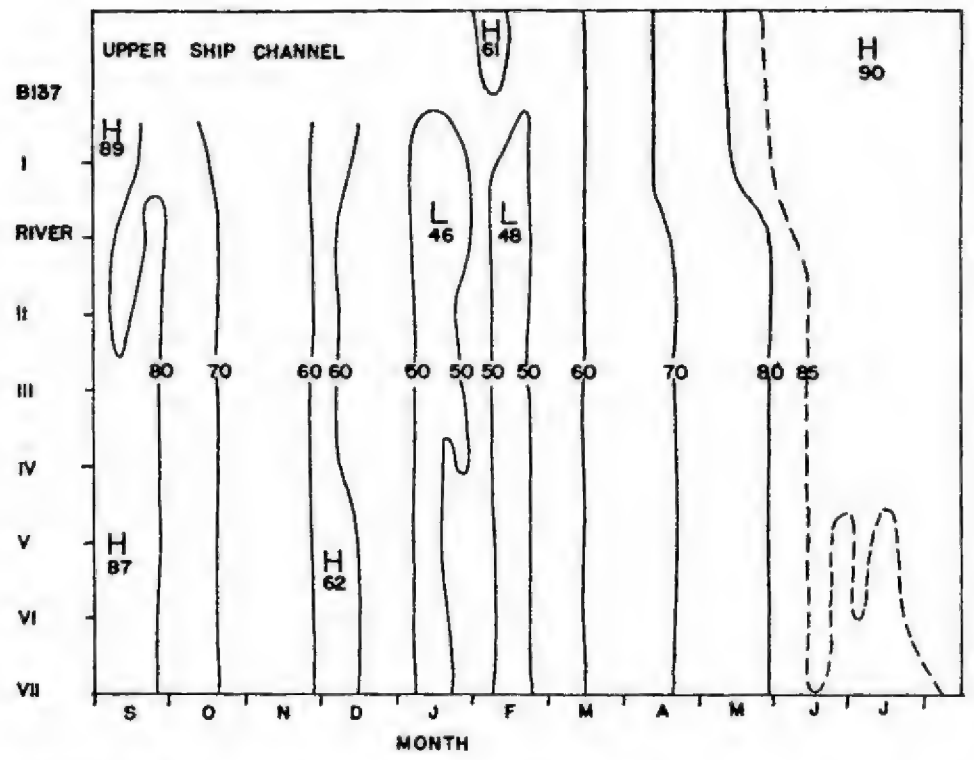
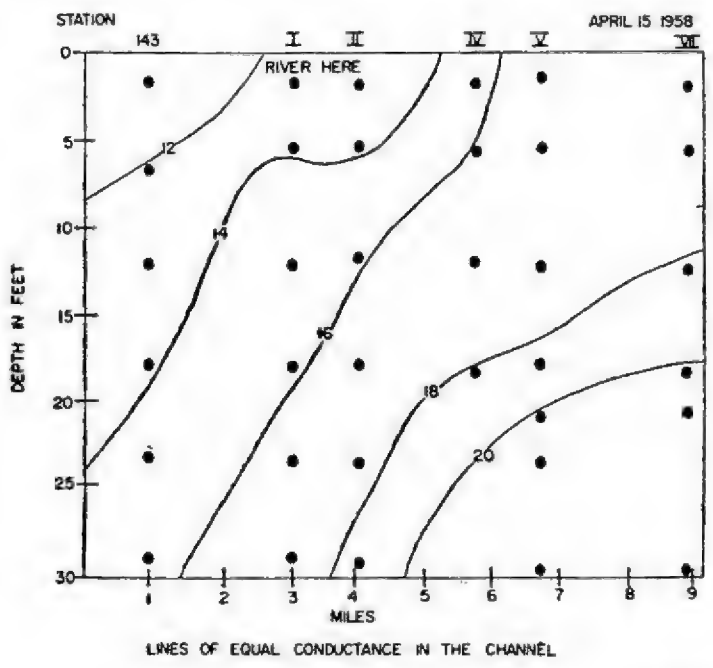


FIG. 8. Temperature of surface water of the Houston Ship Channel in degree Farenheit (°F) and temperature isopleths at 10 degree intervals.



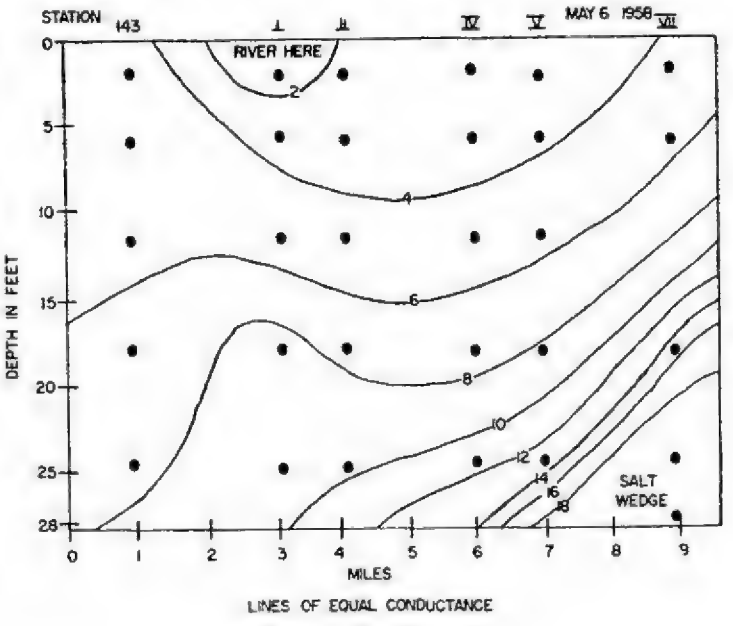


FIG. 9. Lines of equal conductance ($\frac{\text{micromhos}}{\text{cm}} \times 10^3$) in the channel. April 15, 1958.

FIG. 10. Lines of equal conductance in the channel. May 6, 1958.

of the channel for two to three miles. Current velocities indicate that the upper layer of water moving down the channel was pulled into the intake canal of an industrial plant, which lies between Stations IV and V. These data for the channel are representative of the winter condition in which there is sufficient rainfall to cause an appreciable fresh water inflow. Chlorinities of channel samples indicate that the San Jacinto River often shows an appreciable effect over a distance greater than two or three miles downstream and has some effect for a short distance upstream.

The seasonal variation in the hydrography of the area depends to a large extent on the amount of fresh water inflow from the San Jacinto River. The seasonal variation of the San Jacinto River flow is modified by the influence of the Lake Houston Dam on the river and the withdrawal of 92 million gallons of water per day by the City of Houston

TABLE 3

Current data

Date	Time	Location	Method*	Depth	Direction	Velocity, ft./sec.
Jan. 22, 1958	1345	Black Buoy 133	PM	1′	Downstream	0.414
			CC	Surface	Downstream	0.452
	1410	San Jacinto River	PM	6′	Downstream	3.05
	1510	Channel 50 yards east of Burnett Bay	PM	12′	Downstream	1.843
Jan. 29, 1958	1020	Station 2	CC	Surface	300°	0.01
	1050	Station 3	CC	Surface	280°	0.08
	1110	Burnett-Crystal-Cut	CC	Surface	Towards Crystal	0.24
	1150	Narrow Area Crystal-Scott	CC	Surface	.....	0
	1210	Scott-Crystal Cut	CC	Surface	Towards Crystal	0.15
	1215	Scott-Crystal Cut West Side	CC	Surface	Towards Crystal	0.27
	1245	Mouth of Scott	CC	Surface	335°	0.27
	0940	Black Buoy 133, Mid-Channel	PM	15′	Downstream	0.50
	0915	San Jacinto River, Station 10	PM	7′	Downstream	0.863
	1000	Station II, Mid-Channel	PM	15′	Downstream	1.128
	1335	Station IV, Mid-Channel	PM	15′	Downstream	†
			PM	6′	Downstream	0.45
			PM	6′	Downstream	0.35
		Industrial plant intake	CC	Surface	Downstream	0.34
	1300	canal between	PM	15′	Downstream	†
		Stations IV and V	CC	Surface	Downstream	0.365
	1405	Station V	PM	15′	Downstream	†
			PM	6′	Downstream	†
			CC	Surface	Downstream	0
	1425	50 yards east of Black Buoy at tunnel crossing	CC	Surface	Downstream	0

* PM indicates price meter; CC indicates current cross.
† Price meter inoperable due to low velocity.

and the San Jacinto River Authority from the Lake. Thus, as rainfall increases in the fall, the flow rates do not increase proportionately since a large amount is needed to replenish the amount lost to evaporation or withdrawal from Lake Houston through the drier summer months. There is essentially no flow in the river through the drier portions of the year because the withdrawals by the City of Houston are not overcome by the small amount of summer rain. The Lake Houston elevations show that water was coming over the spillway from the latter portion of September through mid-March, intermittently through May, with no flow for June or July.

Flow rate, current direction, D.O., and chlorinity content of the San Jacinto River are shown in Table 4, indicating the seasonal record of fresh water inflow. This fresh water inflow causes considerable seasonal changes in the distribution of salinity in the channel and bays. During the winter months water of low salinity and high D.O. flows into the channel and is highly beneficial since it raises the D.O. content of the channel. Even during the summer period the San Jacinto River flow is beneficial as the ebb flow has a higher D.O. content than the flood flow. After a lapse of time for surface re-aeration and bacteriological activity, a higher quality water returns to the channel.

DISSOLVED OXYGEN DISTRIBUTION IN THE CHANNEL

On several occasions dissolved oxygen concentrations in the ship channel reached low concentrations critical for many living organisms. Dissolved oxygen content usually

varied considerably at a given time in the ship channel between the upper and lower limits of the survey area. All dissolved oxygen determinations with the location and date are listed in Figure 11 and Table 5. Certain representative data are discussed here to show typical conditions in the channel, but the data for any period may be found in Figure 11.

The dissolved oxygen data obtained in the Houston Ship Channel on January 16, 1958, a time of heavy rainfall and subsequent low chlorinities, are presented in Figure 12. It will be seen that the dissolved oxygen at the upper boundary of the sampling area was 2.5 ppm; it then rose to more than 11.0 ppm at the mouth of the San Jacinto River, and dropped only about 2.0 ppm in the remaining 5 miles to the downstream boundary

TABLE 4

Hydrographic data on the San Jacinto River, Station 10

Date	Time	Velocity ft./sec.	Direction Downstream or upstream	D.O. ppm	Chlorinity, ppm
Nov. 14*	0945	1.00	D	9.0	75
Jan. 16*	1000	1.67	U	11.7	39
22*	1345	2.42	D	.....	....
27	1400	0.56	D	10.5	....
30	1100	1.00	D	10.4	25
Feb. 3	1025	1.28	D	10.1	....
6	0950	0.13	D	7.3	540
13	1035	0.77	D	9.7	420
17	1025	.....	....	9.0	....
20	1045	slight flow	U	10.7	2095
24	1107	0.62	D	.....	....
27	1125	1.47	D	9.8	39
Mar. 10	1015	0.28	U	8.1	....
13	1150	0.81	D	7.5	1420
17	0910	0.77	D	5.2	....
20	1115	0.74	D	5.4	3550
21	0950	0.30	U	2.3	3700
24	1010	0.10	U	6.8	....
27	1117	0.16	U	7.1	3266
Apr. 2	1115	0.40	D	2.9	6141
7	0955	0.14	D	6.9	....
10	1007	0.77	D	6.1	3976
15	1115	0.78	D	5.0	....
16	0930	0.41	D	3.2	....
24	1145	0.21	U	6.5	1952
May 2	1200	0.23	D	3.9	2698
6	1200	0.87	D	7.6	....
15	1100	0.46	D	4.3	2840
22	1042	0.69	U	2.0	4583
28	1340	0.31	U	8.1	3284
June 5	1220	0.57	U	1.5	4242
12	1100	0.23	D	4.7	4083
17	1152	0.73	U	2.3	....
26	1300	0.65	D	4.9	3621
July 2	1140	0.51	U	1.9	5041
8	1020	0.08	U	3.5	....
10	1155	0.16	U	3.0	4295
16	1215	0.13	U	.....	....
17	1200	.....	....	2.9	4792
22	1100	.....	....	2.5	....
26	1055	0.52	U	....	....
31	1200	0.13	U	4.7	4508

* Under Highway 73, San Jacinto River Bridge.

TABLE 5

Dissolved oxygen data in ppm at bay stations from September, 1957, through July, 1958

Station		September, 1957								October, 1957								
		3	6	9	13	16	20	27	30	3	7	10	14	16	17	21	29	31
1	°F.	87	85	80	81	81	85	75	74	75	75	75	74	68	69	69	62	68
	D.O.	1.6	1.2	1.9	1.3	1.5	1.3	2.0	1.7	1.1	2.6	2.0	7.3	4.5	5.8	2.9	6.3	2.2
2	°F.	88	85	80	81	81	84	75	73	75	75	75	....	70	70	68	61	67
	D.O.	4.6	1.7	1.2	1.8	2.3	2.6	2.3	3.0	3.5	2.7	2.0	..	3.5	5.6	3.9	7.1	10.5
3	°F.	88	85	80	80	79	85	74	72	75	74	75	....	69	70	66	60	65
	D.O.	4.4	1.6	1.7	4.1	2.1	5.0	2.3	5.0	13.2	5.8	2.0	..	3.9	6.2	6.9	8.4	15.0
4	°F.	87	83	77	78	78	82	71	71	74	74	73	....	69	72	65	58	66
	D.O.	11.6	7.6	5.8	5.4	2.3	7.9	5.3	7.7	11.1	7.7	8.1	..	6.2	7.3	10.6	10.1	12.0
5	°F.	87	83	75	78	80	81	71	70	74	75	73	...	69	72	65	57	66
	D.O.	11.7	8.9	8.1	9.6	3.0	6.5	4.1	7.3	13.2	10.8	9.4	....	9.1	8.5	8.5	12.3	12.0
6	°F.	86	83	76	78	80	83	73	71	75	75	74	....	70	72	65	61	68
	D.O.	10.6	8.5	7.9	8.3	2.7	8.6	4.2	6.1	11.0	9.8	9.1	....	7.7	6.8	7.8	7.3	12.0
7	°F.	86	84	76	77	80	83	71	71	75	75	73	....	70	72	65	68	57
	D.O.	7.1	8.3	6.8	9.1	3.0	8.2	4.1	6.2	8.8	10.0	9.2	....	4.8	6.2	7.4	11.9	15.0
8	°F.	88	85	78	79	81	84	73	72	76	76	74	....	70	73	66	59	69
	D.O.	9.4	5.8	3.9	7.8	5.2	5.0	3.1	4.5	8.9	6.7	6.0	...	4.1	7.3	6.6	9.6	12.0
9	°F.	86	82	76	79	81	....	71	70	75	75	75	...	70	73	65	59	68
	D.O.	11.5	9.0	7.6	10.4	8.3	....	2.2	6.6	9.4	8.6	6.6	...	4.4	6.5	8.0	10.6	12.0

Station		November, 1957						December, 1957								January, 1958						
		4	7	14	18	21	27	2	5	12	16	19	23	26	30	2	9	13	16	23	27	30
1	°F.	70	70	63	65	63	53	52	52	52	60	62	59	60	56	....	....	....	....	....	....	....
	D.O.	4.1	1.8	7.7	8.7	6.5	10.4	9.6	8.1	3.9	5.6	6.1	4.4	3.4	8.1	....	....	....	....	....	....	....
2	°F.	70	70	64	69	63	53	52	53	52	60	62	59	59	57	51	48	50	50	50	..	52
	D.O.	6.0	5.1	6.1	7.8	4.8	10.4	8.4	5.5	3.8	3.6	5.2	6.6	4.9	7.4	6.8	8.1	10.8	11.2	8.2	....	8.9
3	°F.	70	70	63	69	63	53	52	52	50	60	63	59	59	57	47	47	50	51	48	....	52
	D.O.	9.3	6.5	6.8	6.2	5.9	10.9	9.5	9.6	5.7	7.6	6.3	6.4	6.7	7.8	8.9	7.5	12.3	12.3	11.0	....	9.4
4	°F.	70	70	63	69	62	55	..	53	43	60	64	59	59	..	48	45	50	51	48	..	52
	D.O.	10.0	8.6	11.2	7.7	8.4	9.6	.	10.8	12.0	7.9	8.2	8.1	7.3	..	10.2	11.8	14.2	13.1	10.4	..	10.0
5	°F.	69	..	62	69	62	55	.	53	45	60	63	59	58	...	50	43	51	51	47	....	54
	D.O.	9.2	..	7.7	8.2	9.5	9.7	.	10.4	11.0	7.4	8.7	8.8	7.8	....	10.5	12.8	14.4	13.6	11.2	..	12.1
6	°F.	70	....	63	69	62	57	..	55	53	60	64	60	59	..	53	45	51	....	47	....	54
	D.O.	2.2	....	8.5	8.7	10.1	10.4	..	9.8	4.4	5.7	8.0	4.9	8.2	....	9.8	11.7	13.6	....	10.7	....	10.2
7	°F.	69	....	63	69	62	57	51	54	46	60	63	60	60	....	49	44	51	...	47	....	54
	D.O.	8.4	....	7.7	8.7	9.2	10.8	11.7	10.6	12.0	6.0	7.0	7.7	7.3	....	9.4	11.6	14.2	....	11.6	....	9.0
8	°F.	71	...	65	68	62	57	53	55	44	60	64	60	60	57	51	46	51	52	49	....	54
	D.O.	10.9	....	6.5	8.4	8.2	10.9	8.5	7.6	11.2	7.0	7.3	7.6	5.6	8.0	10.5	9.8	11.2	11.9	10.1	....	8.9
9	°F.	71	...	65	69	62	58	52	55	48	60	64	60	60	57	49	45	51	54	50	....	54
	D.O.	10.7	...	7.2	8.0	9.0	10.2	10.6	6.2	7.5	7.0	8.6	6.8	7.4	6.8	9.7	12.8	14.8	13.8	9.7	....	8.8

TABLE 5—Continued

Dissolved oxygen data in ppm at bay stations from September, 1957, through July, 1958

Station		February, 1958							March, 1958							April, 1958					
		3	6	13	17	20	24	27	10	13	17	20	21	24	27	2	7	10	15	16	24
2	°F.	50	59	48	....	48	52	....	63	56	61	60	....	61	63	65	69	69	....	69	77
	D.O.	8.6	5.3	7.4	....	7.5	8.3	....	4.1	12.3	12.1	4.9	....	4.0	8.3	8.5	2.7	5.5	....	1.9	4.2
3	°F.	53	59	44	..	49	....	....	62	56	61	57	....	61	65	66	69	68	....	68	77
	D.O.	9.5	8.9	11.8	....	7.0	....	....	6.8	12.3	12.9	11.6	..	5.7	8.6	12.0	4.4	11.1	....	3.6	6.9
4	°F.	....	59	44	....	....	....	....	62	....	..	58	....	60	63	65	....	....	..	....	79
	D.O.	....	9.5	12.1	....	...	....	....	11.3	....	....	12.8	....	10.5	14.4	9.9	....	.	...	....	8.6
5	°F.	....	59	44	....	....	....	....	63	....	....	58	....	....	60	66	....	....	....	....	79
	D.O.	...	10.2	11.4	...	.	....	....	11.7	.	....	12.8	..	. .	13.5	10.5	....	...	..	....	7.7
6	°F.	....	....	....	....	48	....	....	64	55	....	....	....	....	66	67	....	67	....	67	79
	D.O.	....	....	....	....	10.6	....	....	11.9	14.0	....	....	....	....	15.3	11.7	..	10.1	....	13.5	8.3
7	°F.	....	....	....	..	47	....	....	62	56	....	....	....	60	63	66	67	68	....	68	....
	D.O.	....	.	....	....	11.4	....	....	11.5	12.2	....	....	....	10.4	14.4	10.9	7.8	11.5	....	13.5	..
8	°F.	....	60	....	....	47	...	....	62	56	....	58	....	60	67	67	66	68	....	....	79
	D.O.	....	7.7	....	....	11.0	....	....	12.0	14.0	....	12.8	....	11.6	18.0	13.0	6.4	12.8	....	....	9.6
9	°F.	..	60	45	.	46	....	....	62	57	..	58	....	61	63	65	67	67	....	....	78
	D.O.	....	8.2	12.0	0	10.6	....	....	14.1	13.4	....	13.0	....	12.0	18.0	12.5	7.9	12.2	....	....	6.6

Station		May, 1958								June, 1958				July, 1958						
		2	6	8	15	20	22	27	28	5	12	17	26	2	3	8	10	17	22	31
2	°F.	....	....	....	79	77	78	....	85	88	85	87	86	87	....	85	...	88	88	89
	D.O.	....	....	....	6.6	1.6	2.0	....	4.1	3.5	11.6	3.2	12.6	3.2	....	1.3	....	4.0	3.5	3.9
3	°F.	....	....	....	....	78	79	....	89	88	85	87	87	87	....	83	....	88	87	89
	D.O.	....	....	....	..	1.7	3.3	....	4.6	4.8	8.5	3.6	12.8	3.3	....	8.8	..	4.7	6.8	5.6
4	°F.	....	....	....	79	....	77	....	....	88	85	....	....	85	....	85	84	88	....	....
	D.O.	....	....	....	8.3	....	11.6	....	....	15.0	10.6	....	....	10.5	....	13.0	10.5	12	..	....
5	°F.	....	....	....	80	....	....	..	..	87	86	....	..	83	....	82	84	89	....	....
	D.O.	....	....	..	9.7	....	...	....	..	15.0	15.0	....	....	11.3	. .	8.0	11.6	12.0	....	. .
6	°F.	....	....	77	80	....	....	....	....	....	....	..	...	84	....	83	84	91	...	89
	D.O.	....	....	10.3	6.2	.	....	....	. .	....	....	....	....	10.9	....	8.8	9.8	12.0	....	11.0
7	°F.	....	. .	....	80	75	....	..	....	....	....	..	86	85	....	84	85	88	87	89
	D.O.	....	....	....	9.5	7.5	....	....	....	....	....	. .	13.3	11.6	....	12.4	10.9	12.1	10.9	11.0
8	°F.	....	. .	....	80	....	....	....	..	....	86	....	87	....	....	....	....	89	....	89
	D.O.	....	....	..	10.6	....	....	....	..	..	15.0	....	13.2	. .	....	....	.	12.0	....	11.0
9	°F.	....	....	78	80	....	....	..	....	....	86	....	87	86	....	84	85	....	..	88
	D.O.	....	....	6.6	9.7	....	....	. .	....	....	16.0	....	13.2	13.2	....	12.8	12.8	....	....	10.1

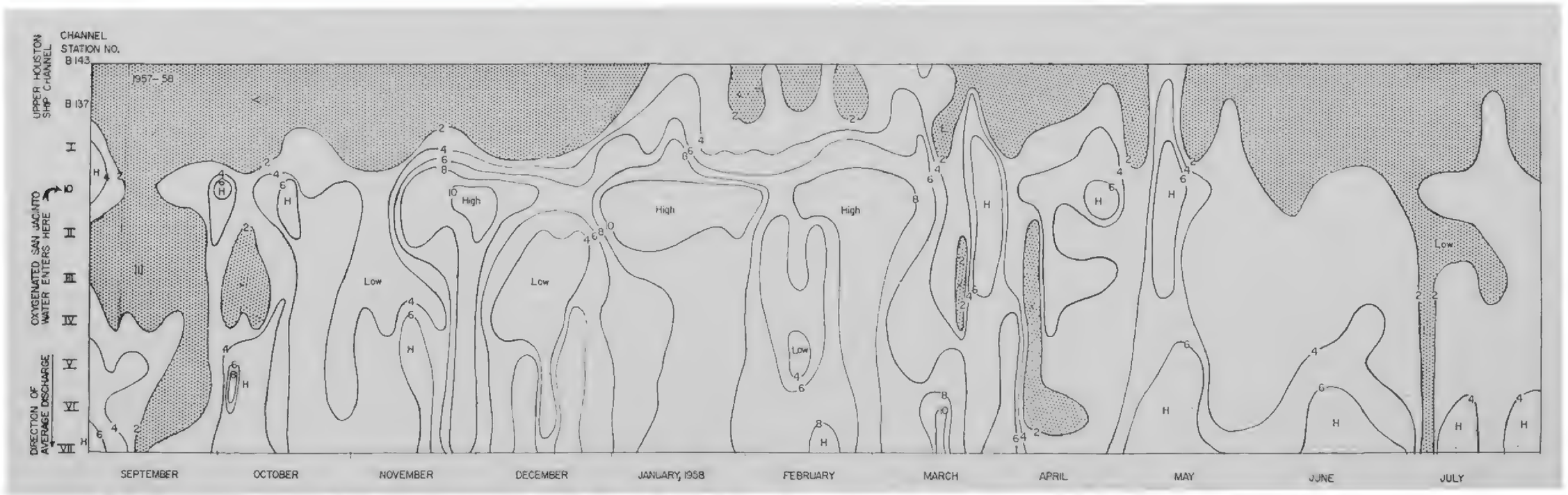


FIG. 11. Concentrations of dissolved oxygen of the Houston Ship Channel in parts per million (ppm) and dissolved oxygen isopleths at 2 ppm intervals.

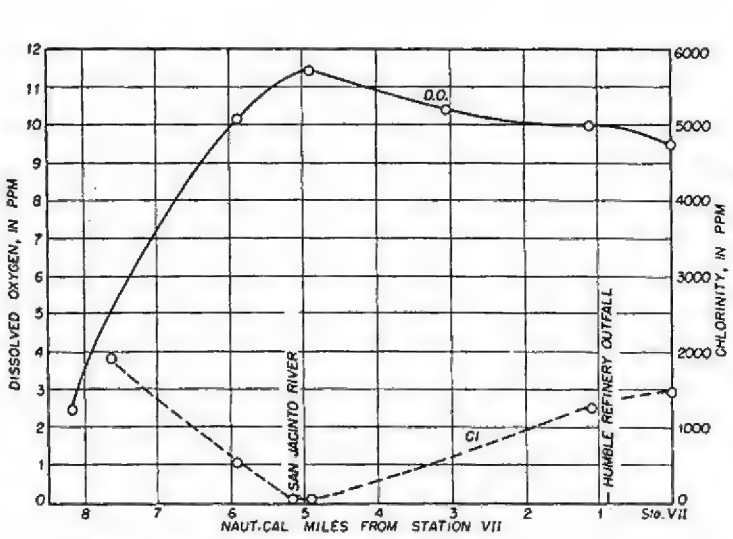


FIG. 12. Dissolved oxygen and chlorinity in the Houston Ship Channel on January 16, 1958, a time of heavy rain and runoff.

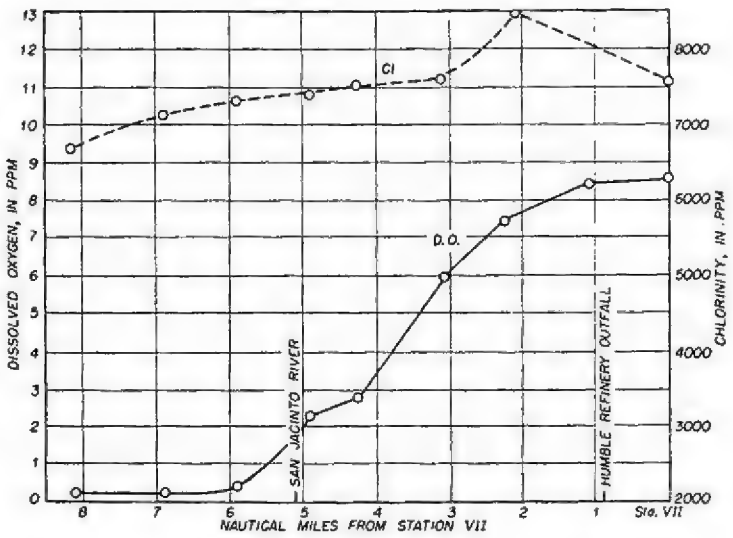


FIG. 13. Dissolved oxygen and chlorinity in the Houston Ship Channel on April 2, 1958, a time of little inflow of river and rain water.

of the survey area. The correlation with chlorinity demonstrates clearly that heavy rains and San Jacinto River flow increase dissolved oxygen in the ship channel.

April 2, 1958, was a time when chlorinities were high throughout the survey area with no rainfall and little flow from the San Jacinto River. For that reason it was selected as representative of hydrographic conditions the reverse of those on January 16, 1958. When the data of dissolved oxygen and chlorinities are plotted against location (Figure 13), we find that after the first mile there was a steady increase in the concentration of dissolved oxygen from the upper to the lower boundaries of the portion of the ship channel. At this time there was very little gradient of chlorinity.

The dissolved oxygen data for July 8, 1958, presented in Figure 14, are representative of the Houston Ship Channel in the poorest condition encountered in regard to dissolved oxygen concentration. On this date the D.O. varied only between 1.0 and 1.5 ppm throughout the part of the ship channel within the survey area. This condition very rarely occurs. Chlorinities were not determined on this date, so the relationship of the phenomenon to salinity is not known. These dissolved oxygen concentrations are below the levels necessary to sustain almost all species of fish.

May 8, 1958, was selected as a day in which the dissolved oxygen concentration was at its highest level throughout the channel. We find (Figure 15) that the dissolved oxygen reached almost 4.0 ppm at the farthest point up the channel, rose above 7.0 ppm at the San Jacinto River, and remained at approximately this level throughout the rest of the survey area. This pattern differs from that on January 16, 1958 only in the higher dissolved oxygen content in the channel above the influence of the San Jacinto River.

SEASONAL PATTERN OF DISSOLVED OXYGEN CONCENTRATIONS IN THE SURFACE WATERS OF THE SHIP CHANNEL

Throughout the portion of 1957 and 1958 in which data are available, we find that there is almost always a greater concentration of dissolved oxygen at the lower end of the area under study than at the upper end (Figure 11). The San Jacinto River when flowing, especially during periods of heavy rainfall, greatly increases the dissolved oxygen content of that portion of the ship channel lying below it and even for a considerable distance above it as was mentioned previously in the discussion of Station I. Partial re-oxygenation by tidal exchange with less polluted water is greater in the lower portion

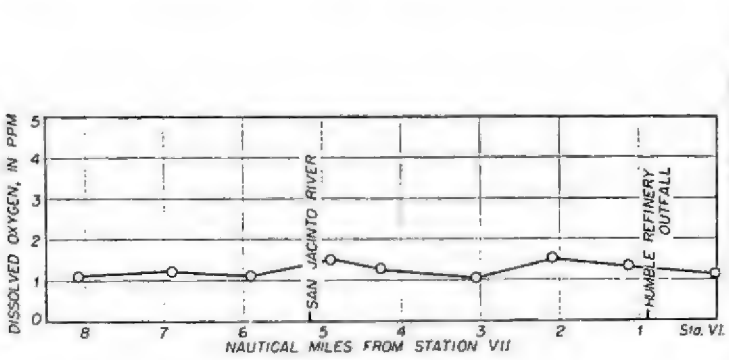


FIG. 14. Dissolved oxygen concentration in the Houston Ship Channel on July 8, 1958, a time of minimum oxygen content.

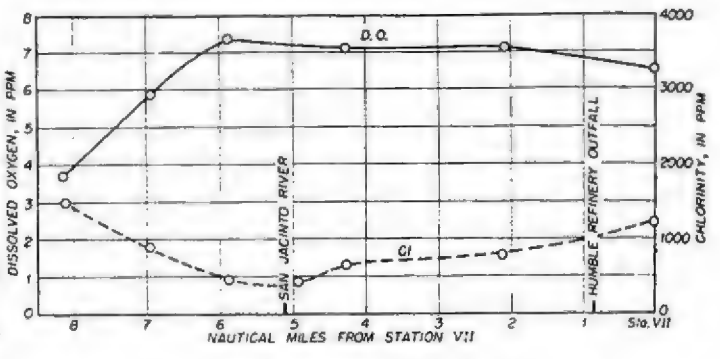


FIG. 15. Dissolved oxygen and chlorinity in the Houston Ship Channel on May 8, 1958, a time of maximum oxygen content.

of the ship channel. The oxygen demands, both biochemical (BOD) and chemical (COD), created by industrial and domestic waste material have a greater effect in the upper channel and are reduced toward the lower channel. Because of the heavy oxygen demands, it is difficult to establish a seasonal picture of dissolved oxygen concentration in the upper channel or to correlate the D.O. with rainfall and salinity. Reference to Figure 16 indicates that in some periods, for example, February, 1958, the D.O. in the upper channel (Station 137) followed the trend of the lower channel (Station VII) though the oxygen content was almost always considerably lower in the upper channel. At other times there was little correlation. During the entire period of study the lower channel (Station VII) dropped as low as 2.0 ppm in dissolved oxygen on only three occasions: September 13, 1957; July 7, 1958; and July 22, 1958. At no time during the survey did the D.O. drop as low as 1.0 ppm at that location.

Station VI, located nearest to the outfall of the Humble Refinery (see map, Figure 3) and approximately one mile above Station VII, has a dissolved oxygen concentration which, when plotted over the year, is found to follow rather closely the curve of Station VII (Figures 16 and 17).

As expected, there is a correlation between the amount of San Jacinto River flow, chlorinity at Station 10, and dissolved oxygen concentration at Station 10 (Figure 18). When the river flow is high, chlorinity is low and dissolved oxygen concentration is high. From a seasonal point of view, the oxygen content rises in winter and drops in summer. Water flowed over the spillway at Lake Houston from September 27, 1957, through December 11, 1957, and from December 13, 1957, until March 14, 1958. There was intermittent flow in the period between March 14, 1958, and April 14, 1958, then spillway flow from April 14 to May 31, 1958. It can be seen in Figure 18 that the period between May 31 and July 31, 1958, in which no flow over the Lake Houston spillway occurred, was the period of lowest dissolved oxygen concentrations at Station 10.

Based on the data obtained in 1957, we can say that the D.O. in the upper channel probably fluctuates independently of seasonal conditions; and that the D.O. at Station 10 is dependent on the flow over the Lake Houston spillway and is highest in the winter, lowest in the summer months, and intermediate in the fall and spring. The lower end of the survey area (Stations VI and VII) has the same seasonal pattern as Station 10. They are influenced by the San Jacinto River, but modified by tidal effects and flow from both the upper channel and the bays.

In July, 1955, prior to this study, a series of dissolved oxygen determinations were made by a modified Winkler technique in approximately the region of the ship channel

in the present study. Oxygen values, as shown in Table 6, were much lower in 1955 than in 1957–58. Possibly the effluents of the industrial concerns and municipal sewage plants above the Battleship Texas (Station I) have been greatly improved or the difference in rainfall between 1955 and 1957–58 resulted in a much improved ship channel from the standpoint of dissolved oxygen content.

Dissolved Oxygen Distribution in the Bays

A series of dissolved oxygen transects across Burnett Bay have been plotted to show typical dissolved oxygen patterns under various conditions. These charts (Figures 19 through 22) have Station II in the channel as the initial point to show conditions in the

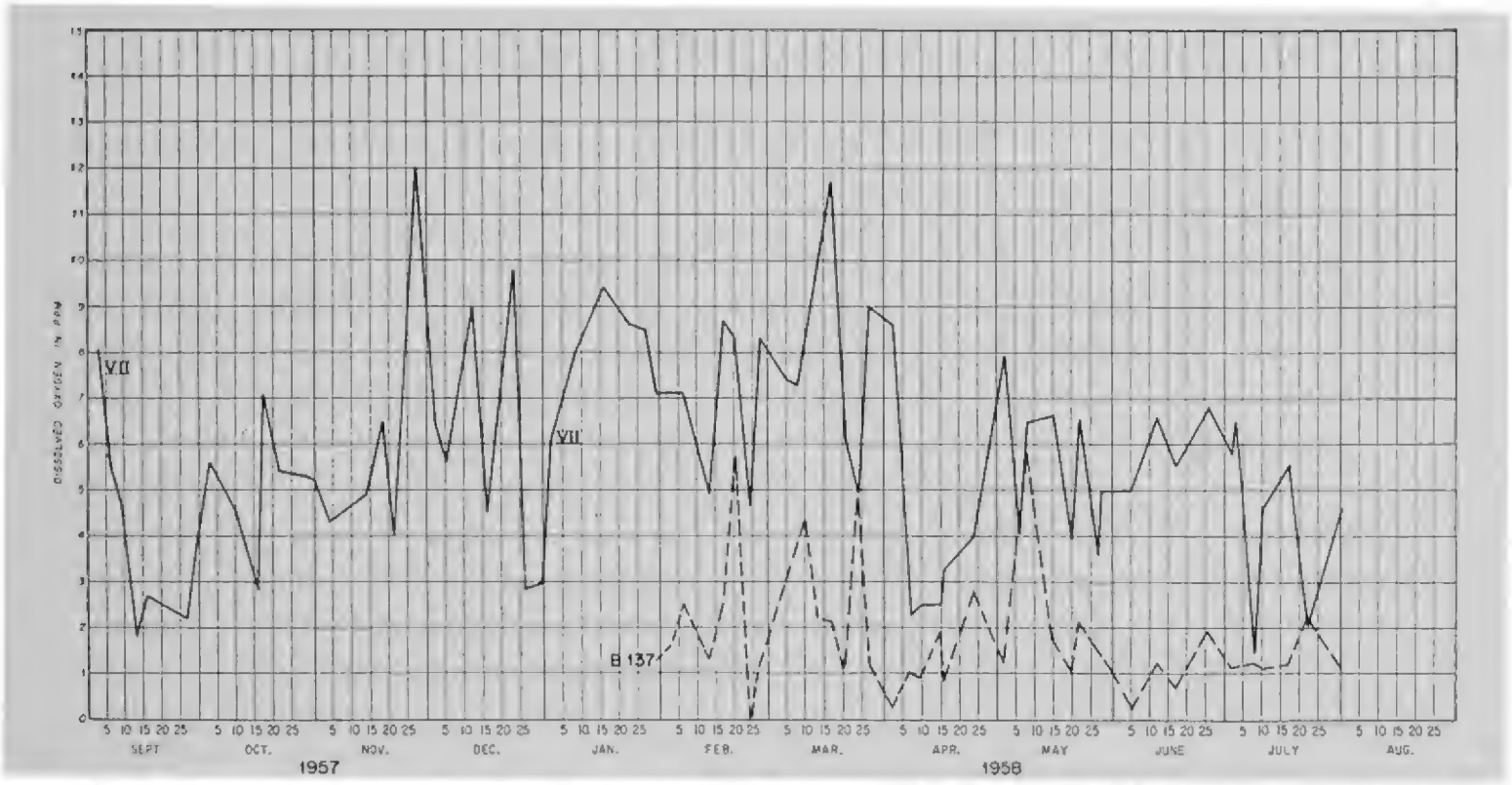


Fig. 16. Dissolved oxygen concentrations in the Houston Ship Channel at the upper (Station 137) and lower (Station VII) limits of the survey area between September 1957 and July 1958.

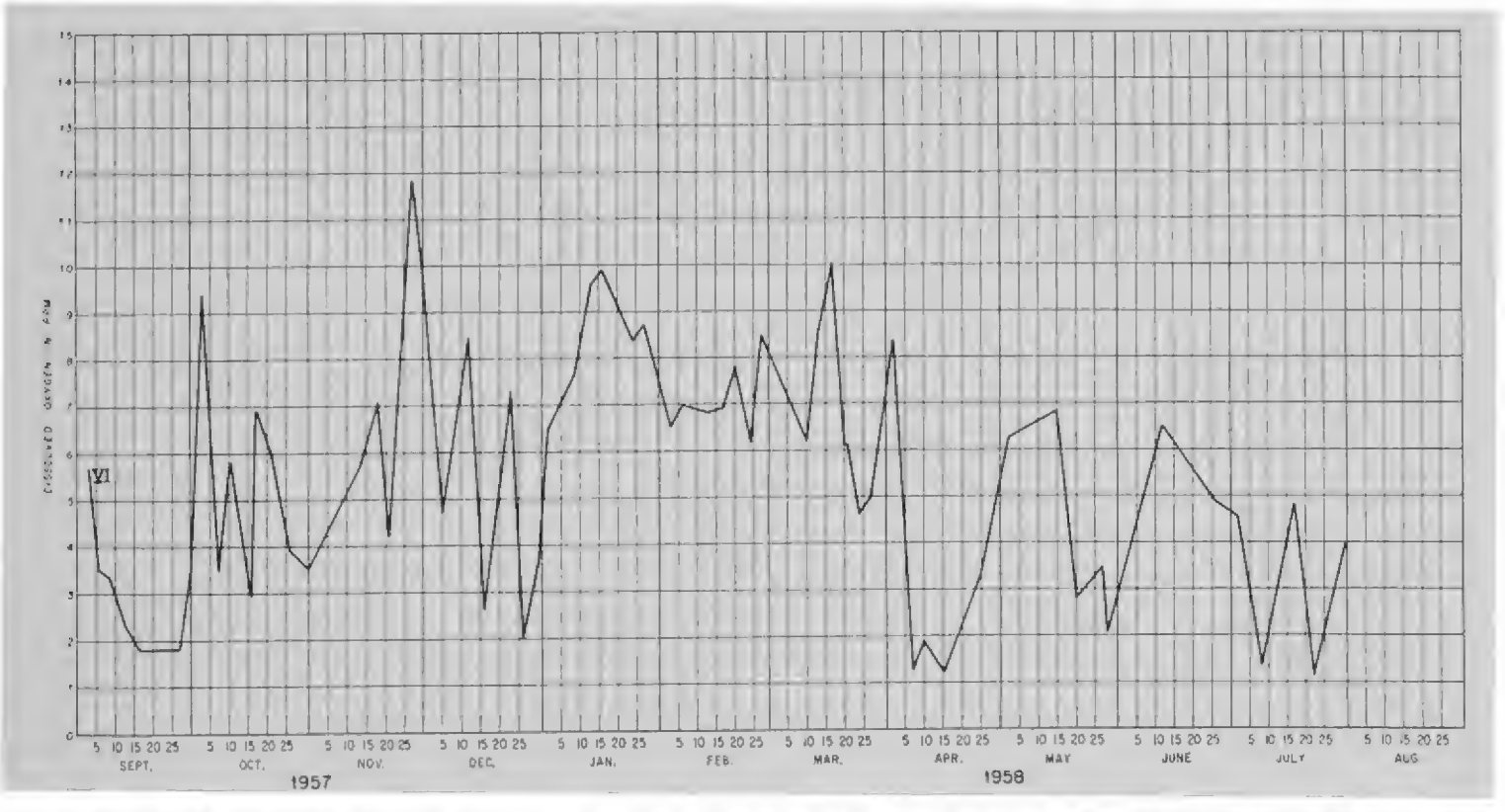


Fig. 17. Dissolved oxygen concentration near the Humble Refinery Outfall (Station VI) from September 1957 through July 1958.

channel, then Stations 2, 3, 7, and 6 (see map, Figure 3) across Burnett Bay to demonstrate changes in the distribution of dissolved oxygen levels relative to distance from the ship channel.

On April 2, 1958, a day typical of those when the salinity is higher in the channel, the

TABLE 6

Dissolved oxygen concentrations at channel stations from July, 1955, through December, 1955
(All data collected at mid-channel)

	Location of sample point						
Date	Battleship Texas	300 yards above San Jacinto River	300 yards below San Jacinto River	Mouth of Peggy's Lake	Power line crossing	Opposite Humble effluent outfall	Tunnel crossing
July 18	1.3	1.4	2.4	4.5	3.5	1.9	1.9
July 21	0.0	0.4	1.2	1.2	1.0	1.9	5.6
July 25	0.0	0.0	0.2	1.7	3.2	0.9	2.0
July 28	0.2	0.6	0.5	1.3	1.6	0.9	1.4
August 1	0.0	0.0	0.3	1.2	1.7	0.9	1.7
August 4	0.1	0.2	0.5	0.9	0.4	2.2	2.7
August 10	0.1	0.0	0.1	0.5	1.0	1.5	1.1
August 17	0.4	0.7	1.4	2.4	2.1	1.8	2.2
August 23	0.0	0.0	0.0	0.3	0.6	0.7	0.7
August 30	0.3	0.7	0.2	1.6	5.7	2.0	3.0
September 7	0.0	0.0	0.6	0.4	0.2	0.9	0.4
September 14	0.4	0.5	0.6	1.3	1.5	1.1	1.8
September 21	0.0	0.2	0.2	1.4	0.7	1.5	1.8
September 28	0.0	0.0	0.0	0.6	2.0	1.1	1.7
October 5	0.0	0.0	0.0	0.0	1.1	1.4	3.3
October 12	0.0	0.0	0.0	0.2	1.1	0.8	1.7
October 19	0.0	0.0	0.0	0.0	1.3	1.6	2.0
October 26	0.0	0.0	0.0	0.0	1.4	1.4	2.8
November 2	0.0	0.0	0.0	0.4	2.3	2.8	3.3
November 9	0.3	0.4	0.5	0.7	2.1	2.3	2.8
November 16	0.4	0.7	0.6	1.1	2.0	2.3	2.6
November 23	0.0	0.2	0.2	0.5	1.5	1.7	2.2
November 30	0.6	0.6	0.6	2.2	5.1	4.4	6.2
December 7	0.3	0.4	0.4	0.5	0.9	0.9	1.9
Nearest station in present survey	I	II (Before Jan. 30)	II (After Jan. 30)	IV	Between V and VI	300 yards below VI	VII

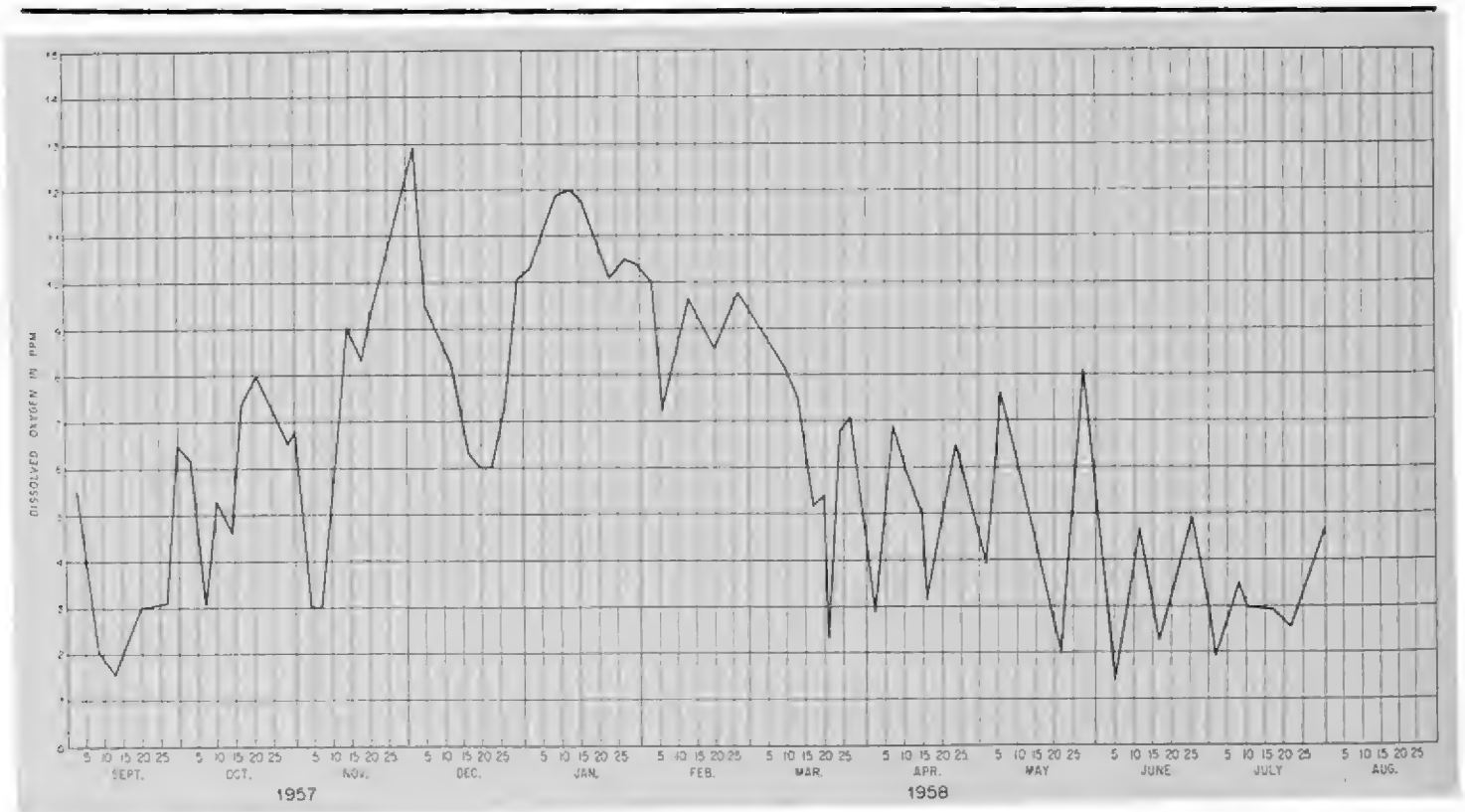


FIG. 18. Dissolved oxygen concentrations in the San Jacento River (Station 10) from September 1957 through July 1958.

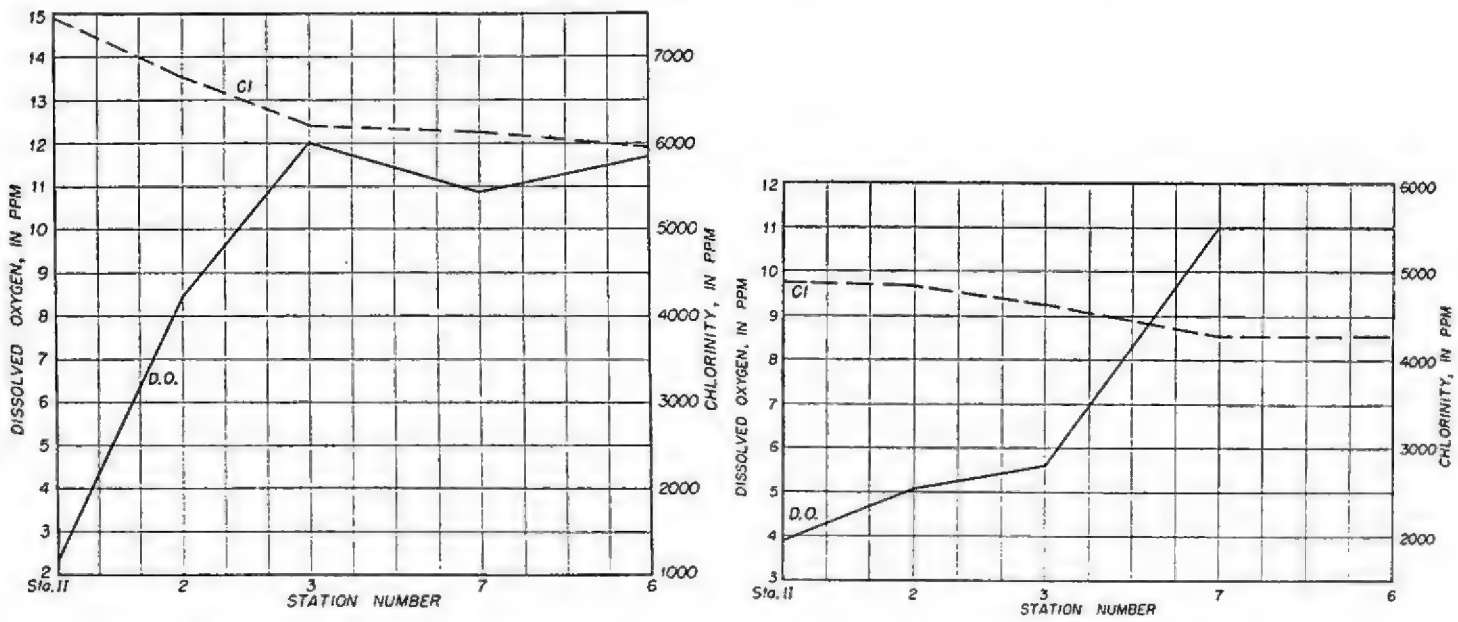


FIG. 19. Dissolved oxygen and chlorinity distribution in Burnett Bay. April 2, 1958.

FIG. 20. Dissolved oxygen and chlorinity distribution in Burnett Bay. July 31, 1958.

oxygen content rapidly increased as the chlorinity gradually dropped (Figure 19). Both dissolved oxygen and chlorinity were essentially constant beyond Station 3 (see map, Figure 3).

On July 31, 1958, the chlorinity of the ship channel and Burnett Bay were very nearly the same. Once again, there was an evaluation of dissolved oxygen across a transition zone (Figure 20).

A situation in which the chlorinities in the bays were higher than in the ship channel existed on December 26, 1957 (Figure 21). This was a time, discussed previously, of high rainfall, heavy river runoff, low salinity, and high dissolved oxygen. Although the dissolved oxygen at Station II in the channel was unusually high, 6.0 ppm, the D.O. continued to increase all the way across the bay. It appears from the chlorinity curve in the figure that little or no mixing occurred beyond Station 2.

The data for October 16, 1958, a period of heavy rainfall, had an oxygen pattern with the dissolved oxygen content high in the channel, low in the transition zone, then high across the bay (Figure 22).

DIURNAL CYCLE OF DISSOLVED OXYGEN

On one occasion, July 8, 1958, after several overcast days, dissolved oxygen content of Burnett Bay water near Station 6 was determined at frequent intervals over a 50-hour period. These data are presented in Figure 23. At 6:00 A.M. on July 8, 1958, the dissolved oxygen content was at the lowest point but soon rose to 20.0 ppm and above with the peak occurring about 5:00 P.M., then the D.O. concentration began to drop. By 7:00 A.M., July 9, however, it had been reduced only to 8.5 ppm, remaining approximately 5.0 ppm higher than it had been at the same time on the previous morning. July 9 was cloudy and the dissolved oxygen concentration did not rise above 11.8 ppm during the day. By 6:00 A.M. of July 10, the D.O. concentration had dropped to 7.1 ppm, 1.4 ppm lower than at the same time the previous morning. July 10, however, was clear and the dissolved oxygen concentration soon built back to saturation. It appears likely that the D.O. concentration would have continued to drop had the cloud cover continued for several more days.

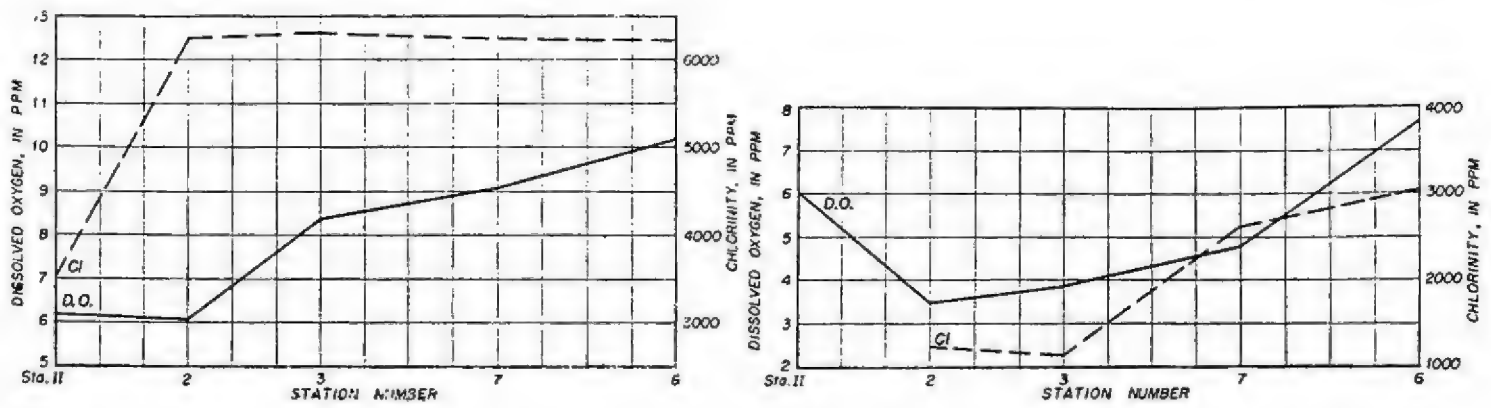


FIG. 21. Dissolved oxygen and chlorinity distribution in Burnett Bay. December 26, 1957.

FIG. 22. Dissolved oxygen and chlorinity distribution in Burnett Bay. October 16, 1957.

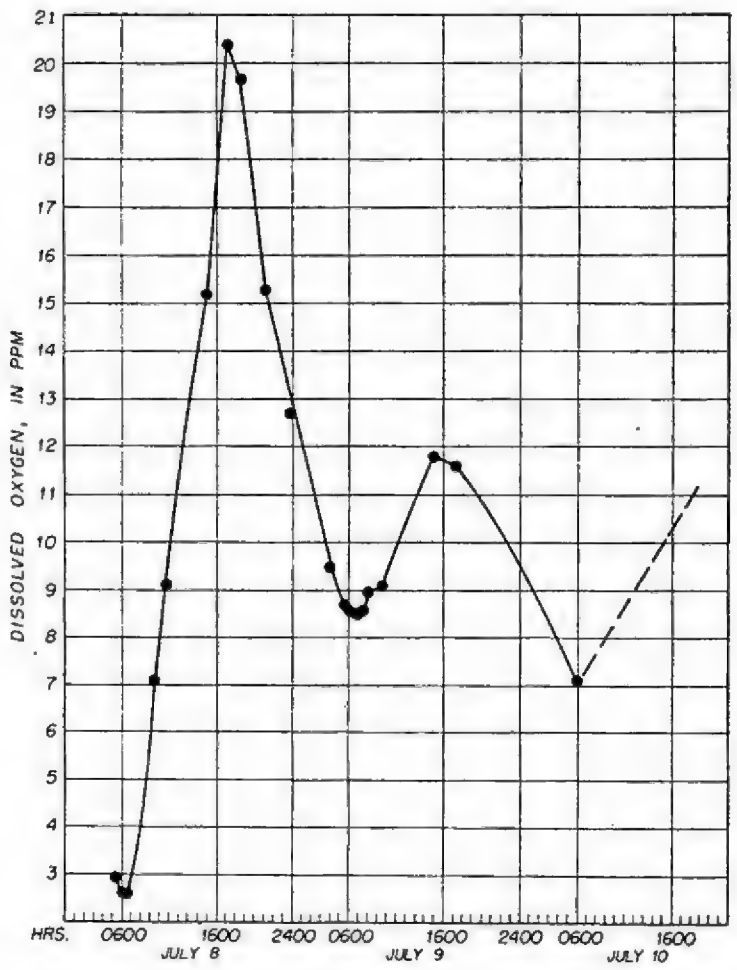


FIG. 23. Dissolved oxygen concentration in Burnett Bay over a 48 hour period.

SEASONAL DISSOLVED OXYGEN CONCENTRATIONS IN BURNETT BAY

In considering the seasonal distribution of D.O. in the bays as shown by the data obtained at Station 7 (Figure 24), two facts must be borne in mind. As discussed earlier, there is a large daily fluctuation in D.O. concentration in the bays and during the year in which these data were obtained rainfall was heavier than for the past several years. Since these data were obtained at approximately the same time each day, they were considered comparable. The general seasonal trend was for the D.O. to be low in the fall, high in the winter, dropping in the spring, and rising again in the summer.

DATA ON OTHER CHEMICAL SUBSTANCES IN CHANNEL WATER

The absence of dissolved oxygen in the Houston Ship Channel from the Houston Turning Basin to the San Jacinto River, a distance of 13.3 nautical miles, indicates that large quantities of organic and inorganic industrial and municipal wastes enter the channel. Seasonal variations and changes in hydrographic conditions have at times ex-

tended the low oxygen conditions of the channel (0.5 ppm) 16.5 nautical miles downstream.

Certain inorganic materials introduced into the channel may actually be beneficial as they accelerate the reduction of the introduced organic material. Phosphate, ammonia, nitrates, and other materials which are needed to support micro-organism populations are introduced into the channel by industrial and municipal wastes. Phosphate is not believed to be a limiting factor in the biological oxidation of organics as large quantities of phosphate enter the channel through its extensive use in the treatment of cooling tower water. The roles of sulfates and nitrates in providing oxygen for the reduction of organic materials are illustrated by data from studies made in the Thames estuary. Nitrates and sulfates in the Thames estuary account for about 8.9 to 10.6 per cent of the oxygen from all sources (calculated from data given by Gameson and Barrett, 1958). In contrast to the Thames estuary, which receives principally sewage wastes, the Houston Ship Channel receives large quantities of industrial wastes and consequently receives a relatively larger quantity of nitrates and sulfates than the Thames. For these reasons it is believed that the quantities of nitrates and sulfates introduced into the Houston Ship channel by industrial wastes play a significant role in preventing the area of dissolved oxygen depletion from being larger than that found.

The evolution of gases which are produced by the bacteriological decomposition of organic materials is clearly visible in the waters above the mouth of the San Jacinto River. Hydrogen sulfide and dissolved oxygen have been determined quantitatively and simultaneously in the upper region of the survey area.

A number of water samples were taken at mid-channel at a depth of about six inches and analyzed for one or several of the following: hydrocarbon, phenol, and sulfide content; chemical oxygen demand (COD), and pH. The results of these analyses are presented in Table 7. Because of the limited chemical data and a realization of the problem of adequately sampling the channel, only a few general conclusions are made.

Considering the large amounts of organic materials that are thought to enter the

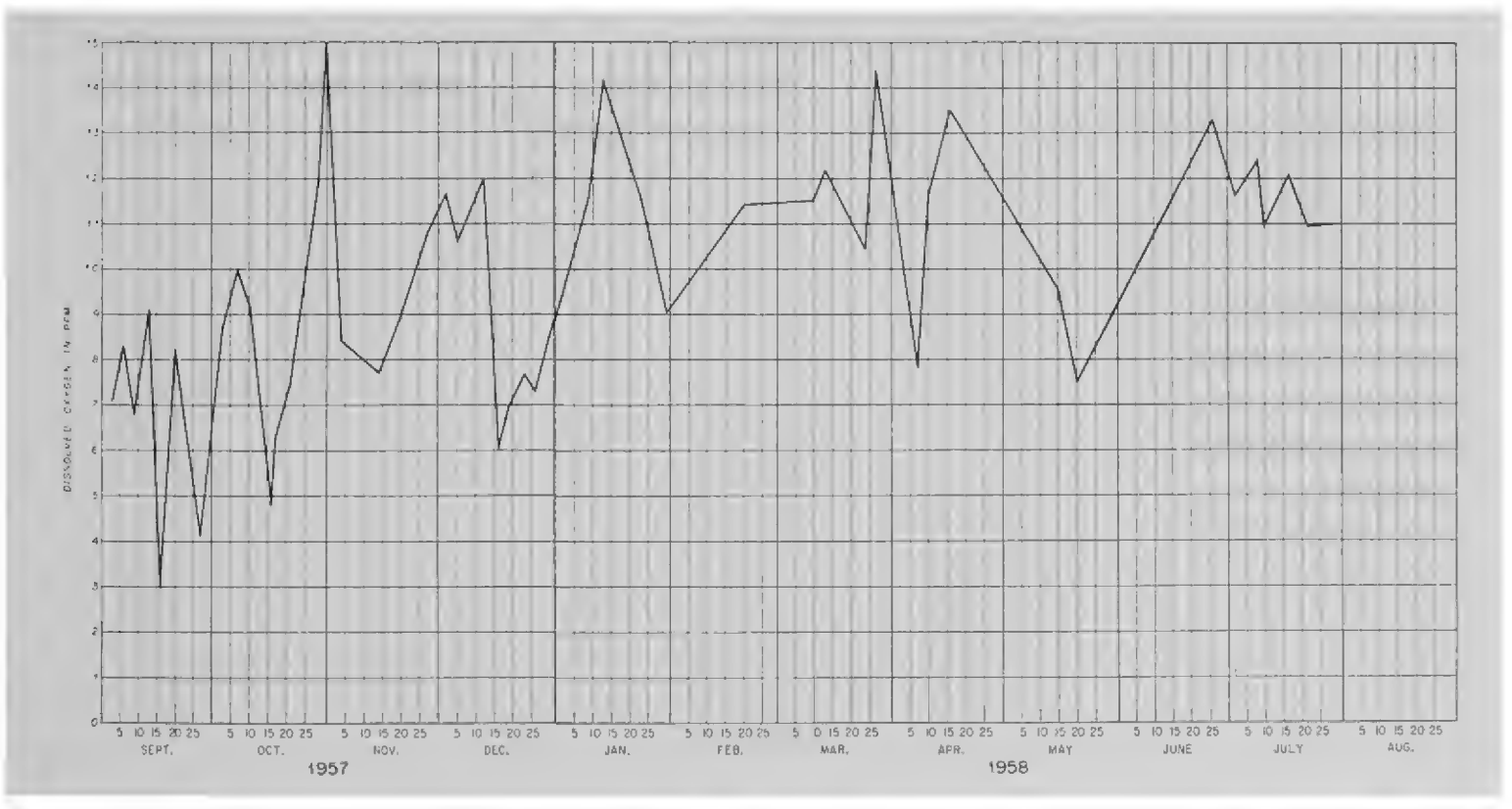


FIG. 24. Dissolved oxygen concentrations in Burnett Bay (Station 7) between September 1957 and July 1958.

TABLE 7

Chemical analysis of channel water

Date	Mid-channel location	Sulfides* ppm	Hydrocarbons† ppm	Phenol‡ ppm	pH	COD§ ppm
Oct. 16	Station No. 1	..	5.0	1.0	.....	....
Dec. 16	Station No. 1	0.0	0.0	0.0	.....	....
Dec. 17	No. 1 Dock	0.0	1.0	0.0	.....	....
Jan. 9	Buoy 141	0.0	4.0	1.0	7.10	....
Jan. 9	Buoy 134	0.0	0.0	....	.....	....
Jan. 16	Buoy 141	0.0	1.0	4.0	7.10	....
Jan. 27	Station No. 1	....	5.9	2.8	.....	....
Jan. 29	Buoy 133	....	2.0	4.0	.....	....
Jan. 30	Buoy 143	....	7.0	14.0	6.86	....
Feb 3	Buoy 143	....	0.0	11.0	7.03	10.0
Feb. 6	Buoy 143	0.0	4.0	13.0	7.06	....
Feb. 13	Buoy 143	....	3.0	7.0	7.09	1.0
Feb. 13	Buoy 137	....	0.0	5.0	.....	....
Feb. 17	Buoy 143	....	0.0	1.0	.....	12.0
Feb. 17	Buoy 137	....	..	....	.....	0.5
Feb. 20	Buoy 143	....	1.0	4.0	7.06	2.0
Feb. 20	Buoy 137	....	1.0	0.0	.....	....
Feb. 24	Buoy 143	....	2.0	1.0	6.92	4.0
Feb. 27	Buoy 143	....	1.0	0.0	6.92	0.5
Feb. 27	Buoy 137	....	1.0	0.0	7.02	....
Mar. 10	Buoy 143	....	0.0	0.0	7.06	4.0
Mar. 10	Buoy 137	....	2.0	1.0	7.07	....
Mar. 13	Buoy 143	0.085	2.0	0.0	7.10	2.0
Mar. 13	Buoy 137	0.085	0.0	0.0	7.32	....
Mar. 17	Buoy 143	0.68	13.0	0.0	7.16	4.0
Mar. 17	Buoy 137	0.25	1.0	0.0	6.98	2.0
Mar. 20	Buoy 143	1.0	2.0	3.0	7.05	....
Mar. 20	Buoy 137	0.5	3.0	1.0	7.07	....
Mar. 21	Buoy 160	0.4	4.0	0.0	6.88	7.0
Mar. 21	Buoy 137	0.8	1.0	0.0	6.97	5.0
Mar. 24	Buoy 143	0.0	....	....	.....	....
Mar. 27	Buoy 143	0.0	....	....	.....	....

Analytical methods:
* Short cut method assuming no mercaptides. Karchmer and Dunahoe (1948), p. 918.
† Simard, *et al.* (1951).
‡ Murray (1949).
§ Chemical oxygen demand, cold permanganate titration. Standard methods for the examination of water and sewage, 9th edition, p. 123.

channel, the hydrocarbon contents determined for upper channel samples (Stations 143 and 137) were surprisingly low.

The pH in the upper channel (Station 143) ranged from 6.8 to 7.2, averaging about 7.0. These data indicate a predominance of acidic material is introduced into the channel since the normal pH range of surface fresh water is 6.0–8.0 and of sea water is 8.0–8.4.

Based on the chemical analysis of channel water for February, March, and April, there was usually at least a 30 per cent reduction in the hydrocarbon, and phenol content between Station 143 and Station 137. The reduced hydrocarbon content at Station 137 could be due to several factors including: (1) the greater dilution by the San Jacinto River water and salt tidal water on Station 137 as compared to 143, and (2) the additional detention time for bacteriological action from Stations 143 to 137. Statistically, there was no correlation between hydrocarbon content and phenol content at either Station 137 or Station 143; correlation coefficients for this being $r = -0.328$ at 137 and $r = -0.06$ at 143.

Bottom Studies

Cores were taken in the ship channel and bays on December 17, 1957. A sketch of the gross appearance of each of these cores is shown in Figure 25. Thick strata of fine grained deposits indicated that the bays were settling basins or areas of deposition. The cores indicated a complex history of deposition, probably the result of repeated dredgings. For example, Core No. 1 showed that the bottom in the upper channel, at Beacon 133, consists of a layer of sand overlaying a three-inch stratum of soft black mud, which rested on a base of fine sand mixed with large amounts of plant debris. Both the lower strata contained many more foraminiferan tests per inch than did the upper sand layer.

A limited number of channel sediment samples were taken with an Ekman dredge 15.2 cm × 15.2 cm, screened, and examined for particulate matter and fauna. The organic content was determined on a previously dried portion of each sample.

The absence of living organisms and the limited amounts of forams, shell, bivalves, and other deposited forms indicate the unsuitable environment for most bottom organisms on the bottom of the channel. Annelids more typical of a normal environment were found only in the shallow areas of the channel in the vicinity of Peggy's Lake.

Particulate material in the form of black conglomerates, possibly oil coated solids or ion sulfide bodies, were more evident in the near vicinity of Humble's outfall and in mid-channel samples from Peggy's Lake and above than in the other areas sampled. The frequency of the black conglomerates seems to be correlated with the organic content of the samples.

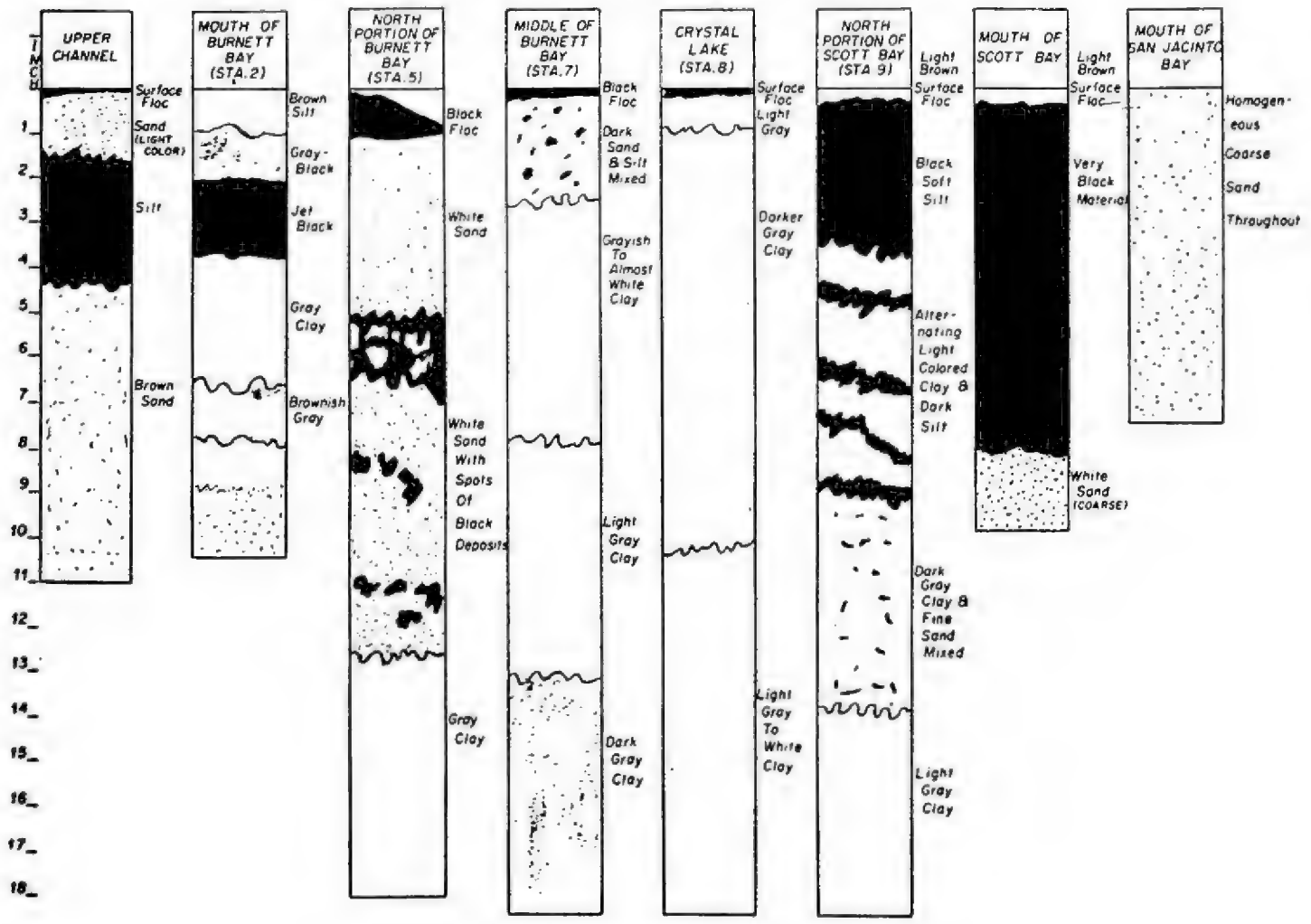


FIG. 25. Sketch of gross appearance of cores.

Organic Content of the Sediments

The organic content of the channel sediments was measured (Table 8) and compared with data on the hydrography of the area, environmental factors, and sources of organic material. Sludge samples were partially dried overnight at 75°C. The dried material was pulverized by a Braun Pulverizer. The infrared spectrum from 2 to 15 microns was determined on CCl_4 extracts of the samples. Because of the complexity and low concentration of organic materials, no compound or type identification were possible from the infrared (I.R.) spectra. The method of determining the organic content using the I.R. spectra as described by Simard *et al.* (1951) was employed on the extracts. The organic content was calculated on a dry sediment basis. There is a 60 per cent reduction in organic content on mid-channel sediment from Buoy 137 to Station IV (4780 ppm to 1920 ppm), a distance of 3.9 miles, and a slight increase in the vicinity of Humble's outfall (2390 ppm), while the organic content 675 yards downstream from the outfall was the same and at 1520 yards the content was higher (3200 ppm). A reduction in the organic content should take place downstream from the source due to conversion by bacterial activity. Reductions under aerobic conditions have been reported as 50 per cent to 80 per cent per week on a mineral oil emulsion (Ludzak and Kinkead, 1956) while under anaerobic condition the reduction is not significant (Ludzak *et al.*, 1957). The greater amount of bacteriological activity, therefore, may take place below the San Jacinto River where there is a more suitable aerobic environment.

The phenomenon of oil breaking from oil coated solids when they are disturbed is well established. The gasification process which occurs in the channel results in a disturbance of the bottom sediments. This action tends to raise the oil and solids toward the surface, with the solids quickly resettling. The reverse procedure also takes place quite rapidly as the oil becomes emulsified by finely divided solids and settles to the bottom again. In an estuary both the solids and oil may generally move downstream while the amount of oil is reduced by biological activity. This movement of oil and sludge is substantially increased by the additional turbulence provided by loaded ocean-going ships moving in the channel.

The rapid emulsification of free oil which then settles, plus the apparent rapid settling of the oil-coated suspended solids, account for the much higher organic content on samples taken at 50 yards from the outfall. As might be expected, organic content downstream is 21,720 ppm while upstream it is 11,800 ppm.

Diversity and Distribution of Fishes and Larger Invertebrates

Discussion and Distribution of the Species

Following are taxonomic lists and discussion of the fishes and larger invertebrates collected by otter trawls in the Houston Ship Channel and adjacent bays. Notes on chlorin-

Table 8

Chemical analysis of channel sediments, June 17, 1958

Location	Organic content, ppm
Mid-channel, 0.75 mile below refinery outfall	3,200
Mid-channel, 0.30 mile below refinery outfall	2,390
Mid-channel, 0.0 mile from refinery outfall	2,390
Mid-channel, 2.20 miles above refinery outfall (Station IV)	1,920
Mid-channel, 6.06 miles above refinery outfall (Station 137)	4,780
50 yards above outfall and 15 yards from eastern shoreline	11,800
50 yards below outfall and 15 yards from eastern shoreline	21,720

ity, temperature, and dissolved oxygen are included with special comments on movement of fresh water and salt water fish in the estuarine area under study. An effort is made to compare the diversity and distribution of biota of the industrialized Houston area with that of other areas studied in the Rockport area by Gunter (1945 and 1950) and in the Galveston Bay area by Reid (1955, 1955a, and 1956).

Penaeus spp.: A total of 5,039 undifferentiated Penaeus were collected in the study. Large numbers of shrimp were present in the bays during August and September, 1957.

Penaeus setiferus (Linnaeus): White shrimp were caught in all bays in which trawls were made; a total of 3,123 taken in the bays and channel were identified as this species. The largest collections were made on July 17, 1958 (1,006) and July 10, 1958 (668). The first shrimp identified as *P. setiferus* appeared on November 14, 1957, as compared to October 10, 1957, for *P. aztecus*. No *P. setiferus* were collected between January 30 and May 2, 1958, migration out of the area apparently having occurred. In other areas Gunter (1950) found that essentially all *P. setiferus* moved out of the bays by the end of December. Chin (1960) shows that white shrimp are always present in Galveston Bay, but that during the winter, shrimp are not abundant in the bay.

Penaeus aztecus Ives: Brown shrimp were collected more frequently and in much larger numbers than *P. setiferus* in the fall and spring. Chin (1960) in the same calendar year found that brown shrimp dominated the bait fishery in Galveston Bay in June. White shrimp first appeared in the fishery in July and became increasingly more important until, in October, brown shrimp comprised only 18 per cent of the catch and had virtually disappeared by November. Our data indicate that *P. aztecus* is much more numerous than *P. setiferus* in the bays in the Baytown area in the fall and spring. The seasonal distribution tends to follow that of Galveston Bay as shown by Chin in that the heavy populations of October (and, presumably August and September) decreased rather rapidly during November, and disappeared completely after December 12, 1957. No *P. aztecus* were collected between December 12, 1957, and May 8, 1958.

Palaemonetes sp.: Grass shrimp were taken on 35 occasions and at all bay stations except between Stations 2 and 3 at the mouth of Burnett Bay, with a total of 489 collected. The maximum numbers were found in December, when 200 were taken in a single trawl in Crystal Lake. No specimens were collected prior to November 27; none were taken in January and the first 20 days of February. The range of conditions over which grass shrimp were caught in the bay was between 44°F and 89.5°F in temperature, and 1.9 ppt to 6.5 ppt chlorinity.

Callinectes sapidus Rathbun: The blue crab is one of the dominant animals in the bays of the survey area. A total of 1,535 *C. sapidus* were collected over a wide chlorinity (190 ppm–7,380 ppm) and temperature range (44°F–89.5°F), being taken in 94 out of the 96 bay trawls.

Data on crabs are related to dissolved oxygen in the environment below.

Dissolved Oxygen Interval	Number of Channel Trawls	Number of Trawls With Crabs	Average Number of Crabs in Catch
0–0.5	3	0	----
0.6–1.0	0	--	. .
1.1–1.5	6	0	....

1.6–2.0	2	1	15
2.1–2.5	8	2	15
2.6–3.0	3	1	3
3.1–3.5	2	1	16
3.6–4.0	2	2	4
4.1–4.5	1	0	. .
4.6–5.0	4	4	23
5.1–5.5	3	3	12
5.6–6.0	3	3	33
6.1–6.5	4	3	8
6.6–7.0	5	5	18
7.1–7.5	1	1	3
7.6–8.0	5	5	5

Few crabs were collected at low concentrations of oxygen. It was noted that when the concentration of D.O. dropped below 1.0 to 2.0 ppm. crabs were observed out of the water on floating objects, or ashore. Carpenter and Cargo (1957) have shown that significant mortality of blue crabs occurred at 28 to 30°C with a 0.86 D.O. and at 24 to 26°C with 0.71 ppm D.O. This ability of *C. sapidus* to exist at much lower concentrations of oxygen than most fishes has been shown by the channel trawls. Often blue crabs were the only animals caught in a trawl. It must again be pointed out that D.O. was determined on samples taken at a depth of about 1 foot while channel trawls were at a depth of five to nine feet where oxygen concentrations may have been lower.

Lepisosteus productus (Cope) : Two specimens of the spotted gar were taken in the survey, both at Station 4–5 in Burnett Bay. One specimen was collected on February 13, the other on March 20, and at a chlorinity of 2.2 ppt and 5.0 ppt.

Lepisosteus spatula (Lacepede) : Twenty-five specimens of the alligator gar were collected in the study. All but five were caught at Station 4–5 in Burnett Bay. All specimens were collected between the months of November and March. Temperature may affect the ease with which they can be caught as no gars have been taken during the warm water period in the summer even though large numbers of gars were seen.

Lepisosteus platostomus (Rafinesque) : Two specimens of the short nose gar were collected in Burnett Bay at 2.3 ppt and 1.9 ppt chlorinity.

Brevoortia sp: The taxonomic keys for the clupeids state the shoulder spots of *B. patronus* is usually followed by one or more additional spots while *B. gunteri* does not have any additional shoulder spots. Those menhaden with shoulder spots taken in this study were tabulated as *B. patronus* while those without additional shoulder spots were tabulated as *Brevoortia sp.* Not one of the specimens tabulated in the field as *Brevoortia sp.* when examined in the laboratory has been identified as *B. gunteri.* The presence of only *B. patronus* is in agreement with Reid (1955). If the menhaden tabulated as *Brevoortia sp.* are, in fact, all *B. patronus,* the per cent range of *B. patronus* without shoulder spots from 0 per cent to 29 per cent for the bays and from 32 per cent to 85 per cent for Station VII (Table 9). One plausible explanation for this significant difference in per cent of *B. patronus* without shoulder spots in the bay as compared to the channel is that generally larger specimens were captured in the bays. It was further noted that the shoulder spots did occasionally appear on specimens that were in the same size class as those without a series of shoulder spots.

TABLE 9

Catch of Menhaden *(Brevoortia patronus)* and the distribution of shoulder spots in 1958

Station	May 22	May 28	June 5	June 12	June 26	July 2	July 10	July 17	July 31
With shoulder spots									
VII	61	.....	21	23	15	30	25	46	68
4–5	.....	.....	71	97	.....	100	95	100	.....
6–7	.....	.....	.....	.....	.....	98	90	100	100
8	.....	.....	.....	100	.....	.....	.....	82	97
9	.....	.....	.....	.....	.....	83	86	.....	.....
Without shoulder spots									
VII	39	.....	79	77	85	70	75	54	32
4–5	.....	.....	29	3	.....	0	5	0	.....
6–7	.....	.....	.....	.....	.....	2	10	0	0
8	.....	.....	.....	0	.....	.....	.....	18	3
9	.....	.....	.....	.....	.....	17	14	.....	.....
Number of Menhaden caught per trawl									
VII	146	300*	132	258	185	235	110	26	334
4–5	.....	.....	41	63	.....	52	55	92	.....
6–7	.....	.....	.....	.....	.....	69	163	37	36
8	.....	.....	.....	4	.....	.....	.....	40	65
9	.....	.....	.....	.....	.....	87	49	.....	.....

* Estimated.

Brevoortia patronus Goode: Thirteen hundred and sixty-two specimens of *B. patronus* were collected at all bay stations and at all channel trawl stations except at Buoy 137. It was present in small numbers in the bays during October and November, but was absent from the survey area between December 5, 1957, and May 8, 1958, when small numbers were collected from the channel at Stations VII and III and between Stations 6 and 7 in Burnett Bay. Beginning in the latter part of May and the first half of June and continuing through July, a large number of *B. patronus* were found in the channel and in the bays. It was never taken above the mouth of the San Jacinto River in the trawls. This form was found in the bays in a wide chlorinity range, from 1,030 ppm to 6,600 ppm, but was most abundant at a chlorinity range of 3.9 ppt to 5.2 ppt.

Reid (1955) found that East Bay supported a large population of this species, although it had been considered the high salinity form of the genus in the past. Gunter (1945) found a peak abundance of *Brevoortia sp.*, which he felt included *B. patronus* and another species, in April and a low point in June and July. This is in contrast to our data which show the greatest abundance during this time. Our data agree with Gunter's data showing an exodus of this form from the bays in mid-winter.

Dorosoma cepedianum (LaSueur): The gizzard shad was taken over a wide range of temperature and chlorinity as shown by its presence in 92 of the 96 bay trawls. A total of 6,903 specimens of this species have been collected. The population increased in the fall until the winter trawl samples taken from November through February were composed chiefly of gizzard shad. The monthly catches are shown below:

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
Bay Trawls	10	12	13	17	8	9	8	5	3	11
Trawls With Catch	10	12	13	17	8	6	7	5	3	11
Number of Fish Per Catch	15.3	64.4	54.1	213.4	92.5	8.0	13.7	25.8	16.0	25.9

Since the gizzard shad has been reported to spawn in fresh water in the spring, the high winter population in the bays may be the result of migrating through the area from Galveston Bay to spawn.

The much smaller catches in the channel may be correlated with low oxygen concentrations there. The lowest concentration of oxygen at which gizzard shad were caught was 4.6 ppm and of the 20 trawls taken at 4.6 ppm or above, shad were taken in 6 of them.

Dorosoma petenensis (Günther): The threadfin shad, formerly in the genus *Signolosa*, was found to be a common fish in the area, a total of 742 being collected. The threadfin shad, like the gizzard shad, was found over a wide range of temperature and chlorinity (0.19 ppt—7.4 ppt), but it was not found as abundantly nor was there a high winter population. These generalities can be seen in the monthly catches shown below:

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
Bay Trawls	10	12	13	17	8	9	8	5	3	11
Trawls With Catch	9	11	10	13	5	3	6	3	1	1
Number of Fish Per Catch	13.8	19.9	9.2	6.1	8.0	1.4	3.9	3.0	0.3	0.1

The lowest concentration of D.O. in the channel at which threadfin shad were caught was 4.6 ppm which was the same minimum concentration at which gizzard shad were collected.

Anchoa mitchilli Hildebrand: On August 20–21, 59 specimens of the bay anchovy were taken in Burnett Bay. Subsequently it was collected 10 times, a total of 19 specimens, but only a few specimens were taken after October 31, 1957. Reid (1955) found this species to be third in number of fishes caught in East Bay, but he states it is probably the most abundant fish in the bay.

Ictiobus bubalus (Rafinesque): A single specimen of smallmouth buffalo was taken by trawl, three times in Burnett Bay and once in Scott Bay. All specimens were taken in December and January when the water temperature was between 44°F and 54°F. Chlorinities ranged between 0.5 ppt and 3.2 ppt, when they were collected.

Cyprinus carpio Linnaeus: One specimen of this fresh water carp was taken on November 14, 1957 in Scott Bay at a chlorinity of 2.5 ppt, a temperature of 65°F, and a dissolved oxygen content of 8.0 ppm. Neither Gunter (1945) nor Reid (1955 and 1956) list this species as occurring in Texas bays. Breder (1929), however, lists it as an occasional stray in Chesapeake and New York bays.

Bagre marina (Mitchill): Gafftop catfish were collected in Scott Bay, in September and on July 10, 1958, at chlorinities from 4.4 ppt to 4.9 ppt.

Galeichthys felis (Linnaeus): Large numbers of sea catfish were taken in Scott Bay in the collections of August 20–21, 1957. This species remained common in the bays until October. It was not taken from December until March 20, 1958, and it was not common again until June.

Ameiurus melas (Girard): Two black bullheads were taken in Crystal Lake (October 31, 1957, chlorinity 2.9 ppt, temperature 69°F; December 26, 1957, chlorinity 6.1

ppt, temperature 60°F). This species was found in the bays during the winter when the chlorinity was reduced by heavy rains.

Fundulus grandis Baird and Girard: Because of the preference of the gulf killifish for shallow water, numbers in trawl collections were not a true indication of the numbers of *F. grandis* in the bays. It was taken on 18 occasions, with a total of 50 specimens collected.

Fundulus similis (Baird and Girard) : Two specimens of longnose killifish were collected between Stations 4 and 5 in northern Burnett Bay on December 26, 1957.

Cyprinodon variegatus Lacepede: The broad killifish was caught in the trawls on 14 occasions with a total of 69 specimens being taken. It was collected in all the bay stations except between Stations 6 and 7 but was never taken in the ship channel. The hydrographic conditions in which it was collected were about the same as those for *F. grandis.*

Strongylura marina (Walbaum) : Two needlefish were collected on September 27, 1957, at Station 8 in Crystal Lake.

Urophycis floridanus (Bean and Dresel) : A single specimen of the southern hake was taken in Burnett Bay on April 2, 1958 at a chlorinity of 6.1 ppt.

Menidia beryllina (Goode and Bean) : The gulf silverside was collected in six different trawls with a total of 10 specimens taken. Large schools have been noted moving up the channel during the months of June and July. Chlorinities were quite variable, but temperatures were fairly low—ranging from 44° to 58°F.

Mugil cephalus Linnaeus: The striped mullet is unquestionably the dominant fish in the survey area. On many occasions no specimens were taken in the trawl when the surface of all the bays were virtually alive with mullet. It would be impossible to estimate the number or weight of mullet, most of which are *M. cephalus,* in bays of the survey area, but the figures would undoubtedly be extremely large. Despite the inefficiency of the otter trawl in collecting mullet, *M. cephalus,* with 1380 caught, ranked fifth, after *D. cepedianum, M. undulatus, L. xanthurus,* and *B. patronus,* in number of specimens of fishes collected in the study (Table 10). It was taken at all stations and under a wide range of hydrographic conditions.

The mullet was taken over the entire chlorinity range of the bay trawls while the majority were caught in water below 4.0 ppt chlorinity. Only three successful catches of mullet were made out of 19 trawls in May, June, and July. Since temperature apparently affects the susceptibility to capture of this species, trawl samples cannot be used as indices to the actual population. The catch by month is indicated below:

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
Bay Trawls	10	12	13	17	8	9	8	5	3	11
Trawls With Catch	7	10	11	17	7	7	7	2	1	0
Number Per Catch	4.4	24.0	2.3	37.9	17.6	9.5	4.4	0.4	2.7	0
Temp. Range of Catch Trawls	66–73	55–65	44–60	44–54	44–60	56–64	65–78	78–80	86	

Whether the variations are real or due to interaction of temperature upon the catch per trawl is not certain.

TABLE 10

Abundance of shrimp, crabs, and the 20 most abundant species of fish in trawl collections from October, 1957 through July, 1958

		Total numbers caught
Dorosoma cepedianum	gizzard shad	6,903
Micropogon undulatus	croaker	3,960
Penaeus setiferus	white shrimp	3,123
Brevoortia patronus	gulf menhaden	2,935
Leiostomus xanthurus	spot	2,330
Penaeus sp.	commercial shrimp	2,199
Leiostomus and *Micropogon*	spot and croaker	1,748
Penaeus aztecus	brown shrimp	1,746
Callinectes sapidus	blue crab	1,535
Mugil cephalus	striped mullet	1,380
Dorosoma petenensis	threadfin shad	742
Palaemonetes sp.	grass shrimp	489
Cynoscion arenarius	sand trout	262
Pogonias cromis	black drum	86
Cyprinodon variegatus	broad killifish	69
Fundulus grandis	Gulf killifish	50
Galeichthys felis	sea cat	32
Lepisosteus spatula	alligator gar	22
Anchoa mitchilli	bay anchovy	19
Lagodon rhomboides	pinfish	18
Bagre marina	gafftopsail catfish	16
Aplodinotus grunniens	freshwater drum	15
Stellifer lanceolatus	star drum	14
Dormitator maculatus	sleeper	14
Pomoxis nigro-maculatus	black crappie	13
Menidia beryllina	gulf silverside	10

Mugil curema Cuvier and Valenciennes: The white mullet was rare in the survey area, only two specimens being taken on October 10, 1957.

Polydactylus octonemus (Girard): The eight-fingered threadfin was collected only once when six specimens were taken on May 15, 1958, in the Houston Ship Channel (Station VII).

Trichiurus lepturus Linnaeus: A single specimen of cutlass fish was collected in each of three trawls at Station VII in the Houston Ship Channel. Chlorinities at the time of the collections were 7.4 ppt, 4.5 ppt, and 5.2 ppt.

Pomoxis nigro-maculatus (LeSueur): In the present study the black crappie was collected on 10 occasions, with a total of 13 specimens taken. It was found in Burnett Bay, Crystal Lake, and Scott Bay and in the Houston Ship Channel at Station III and as far down the channel as Station VII from December through April. It was found at chlorinities as high as 6.8 ppt.

Lepomis microlophus (Günther): A single redear sunfish was captured on January 9, 1958, between Stations 4 and 5 in Burnett Bay at a chlorinity of 3,180 ppm.

Chaenobryttus gulosus (Cuvier): On December 12, 1957, and April 24, 1958, a warmouth bass was collected from Burnett Bay at chlorinities of 5.9 ppt and 5.0 ppt.

Roccus chrysops (Rafinesque): One specimen of white bass was collected between Stations 6 and 7 in Burnett Bay on December 26, 1957, at a chlorinity of 6.2 ppt.

Roccus mississippiensis (Jordan and Evermann): Yellow bass were collected on three occasions in Burnett Bay, October 10, December 12, and January 30 where chlorinities ranged from 2.9 ppt to 5.2 ppt and the temperature from 44°F to 73°F.

Lagodon rhomboides (Linnaeus): In August and September, 1957, 250 pinfish were collected, mostly in Crystal Lake. The species disappeared from the area by the first of November and was not taken again until the latter part of June, an absence of almost seven months.

Gunter (1945) found *L. rhomboides* to be absent from Copano from December to March inclusive.

Larimus fasciatus Holbrook: Two banded croakers were collected on August 20, 1957, in Burnett Bay.

Stellifer lanceolatus (Holbrook): Star drum were collected during October and November, 1957, but were not taken from November 14, 1957, until July 10, 1958. The chlorinity at which it was collected ranged from 370 ppm to 6,000 ppm and the temperature varied from 63°F to 85°F.

Sciaenops ocellata (Linnaeus): Four redfish were taken during the study.

Leiostomus xanthurus and *Micropogon undulatus*: The two species of commonly found croakers are discussed together because of the similarity of their life history and the difficulty in distinguishing the smaller juveniles.

The spot is one of the most common fishes found in the survey area. It was abundant at the time of the preliminary sampling during August and September, 1957, and continued to be found in small numbers in Burnett, Crystal Lake, and Scott bays during October. It was absent from the end of October until the first of May, except for large numbers of very small fish which were difficult and often impossible to separate from the young of *Micropogon undulatus*. A total of 1,748 of these mixed young were collected between January 9, 1958, and April 24, 1958.

After the young became large enough to be readily identified, the numbers of spot collected increased greatly, with large numbers being taken at all bay stations and in the lower ship channel. A total of 2,330 spot were collected and identified during the study.

Reid (1956) found this to be one of the most abundant fishes in East Bay. Gunter (1945) caught large numbers of *L. xanthurus* in Copano and Aransas bays within wide ranges in temperature and salinity, but caught few specimens during the winter months.

In the present study 3,960 croakers were caught and identified as *M. undulatus*, and as discussed, large numbers of young were collected but not distinguished from *L. xanthurus*. Recognizable *M. undulatus* were absent from the area during the latter half of November and all of December and January. Fish identifiable as *M. undulatus* appeared in the bays in February and became numerous in April. Large populations were present through the end of July, 1958.

The monthly catch of spot and croaker, as tabulated, illustrates the decline of the population in the fall, absence from November 14 to January 16, and an increase in the spring. Thousands of small croakers were seen in the channel as early as December 16. They were undoubtedly also present in the bays by this time but were too small to be taken by otter trawl. Size ranged from about 11 to 200 mm for croaker and 16 to 100 mm for spot.

	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
Bay Trawls	16	10	12	13	17	8	9	8	5	3	11
Catch Per Trawl	5.2	1.9	0.1	0.0	0.7	1.6	10.9	231.1	287.2	66.0	140.4

The last *L. xanthurus* to be taken in the fall was on October 31, while some two weeks later on November 14 the last *M. undulatus* was taken.

There is some evidence that the D.O. requirements for the two species may be different. The spot was found at lower concentrations of D.O. than the croaker. The ratio of spot to croakers for the bay trawls and two of the channel trawls for the months of May, June, and July are given below:

Ratio of Species	Location	May	June	July
L. xanthurus/M. undulatus	Bay	0.01	0.83	0.51
L. xanthurus/M. undulatus	VII	0.93	0.36	5.37
L. xanthurus/M. undulatus	III	4.72	(11/0)	(0/0)

The higher ratio of spot to croaker in the channel as compared to the bays for May and July and the difference in the ratio between the channel trawls for May and June indicate a difference in D.O. requirements for the two species.

Th spot and croaker were usually taken in the channel when the D.O. content was above 3.7 ppm. Of the 40 trawls made during this period the fish were taken in 17 out of 18 trawls when D.O. was above 3.7, but when the D.O. was lower than 3.7 ppm, fish were taken only once in 22 trawls. At 2.0 ppm only *L. xanthurus* were caught.

Pogonias cromis (Linnaeus): Drum were found in small, but consistent, numbers through November until April when the species disappeared completely from the collections. *P. cromis* was taken at chlorinities from 370 to 6,780 ppm.

Cynoscion arenarius Ginsburg: Sand trout were relatively abundant in all the bays until late November. No *C. arenarius* were taken during the months of December, January, February, and March as shown by the monthly catch below:

	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
Catch Per Trawl	6.5	2.7	0.5	0	0	0	0	0.1	0.2	2.0	16.0

It has been shown by Gunter (1945) and other workers that there is a decline of the bay population in the fall and winter and that the sand trout apparently migrates to the gulf at the onset of cool weather in the fall. The lowest temperature at which fish were caught by Gunter (1945) was 66.9°F (13.7°C). In this study, however, fish were taken in late October and November at water temperatures somewhat lower than 67°F. For example, in eleven trawls in the spring, trout were caught in a temperature range between 62° to 68°F.

Cynoscion arenarius were taken over a wide salinity range as shown below:

Cl Interval,	0	0.5	1.0	1.5	2.0	2.5	3.0	3.5
ppt	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
Bay Trawls	9	6	3	9	10	3	4	7
Catch Per Trawl	0.0	0.0	1.0	1.2	1.7	0.0	0.0	2.0
Cl Interval,	4.0	4.5	5.0	5.5	6.0	6.0	6.5	7.0
ppt	4.5	5.0	5.5	6.0	6.5	6.5	7.0	7.5
Bay Trawls	10	8	9	6	8	8	3	1
Catch Per Trawl	6.7	6.5	51.5	9.0	1.0	1.0	10.0	0.0

Sand trout were probably absent in the middle chlorinity range and below 1.0 ppt because all the trawls except one in these particular intervals were taken at a temperature lower than 62°F.

After the water temperature rose above 62°F, sand trout were taken in seven out of 15 trawls at Station VII while none were taken at Station III where 11 of 14 trawls made were in water below 4.0 ppm D.O.

Cynoscion nebulosus Cuvier and Valenciennes: The speckled trout was taken only once during the survey.

Aplodinotus grunniens Rafinesque: The fresh water drum was collected on 11 occasions with a total of 15 specimens taken sporadically during the months of October, November, January, March, and April. The chlorinity at which fresh water drum were taken in the bays ranged from 40 ppm to 6,500 ppm and the temperature varied from 49°F to 84°F. It was found on seven occasions at chlorinities above 1.0 ppt and on three occasions above 5.0 ppt.

Chaetodipterus faber (Broussonet) : Spadefish were found in August and September, 1957, with a total of 18 collected. The species was not collected between September and July 31, 1958.

Dormitator maculatus (Bloch) : The sleeper was first taken during the preliminary study in September, 1957, when 28 specimens were taken in all the bays in the area. Fourteen specimens were taken in the survey from October until the middle of December, 1957. It was not taken after December 12, 1957, at any station. Chlorinities varied from 0.19 ppt to 6.6 ppt; the temperature ranged from 44°F to 73°F.

Gobioides brousonneti Lacepede: The violet goby was collected on five occasions from Burnett Bay, Crystal Lake, and Scott Bay with a total of seven collected. Chlorinity ranges at the time of collection varied from 1.4 ppt to 6.6 ppt. This form was taken in October, December, and February.

Gobionellus shufeldti (Jordan and Eigenmann) : Four specimens of this fresh water goby were collected during October, November, and December, in Crystal Lake on three occasions. Chlorinity varied from 1,950 ppm to 5,970 when they were taken. Neither Gunter (1945) nor Reid (1956) collected *G. brousonneti* or *G. shufeldti.*

Trinectes maculator (Bloch) : The hog choker was taken on five occasions in the survey, all in Burnett Bay between October 31, 1957, and January 30, 1958. Chlorinities varied from 0.34 ppt to 5.2 ppt and the temperature range was from 49° to 66°F.

Variation in Trawl Catch Between Stations

To determine if a significant difference existed in the trawl samples at stations, the sign test was employed. The catch per trawl for each species at a particular station was compared during a two-week period, in most cases for each of the two weeks, to the catch per trawl at the other bay stations.

The results of such comparisons indicate no significant difference exists in the catch between the individual bay trawls except that, on occasion, the sample taken in the entrance of Burnett Bay (Station 2 to Station 3) was significantly different from the other bay trawls.

Scott Bay is much closer to the point of discharge of the Humble effluent than stations in Crystal or Burnett bays. Since trawl data in Scott Bay were not significantly different from that in the other bays, it is believed that Humble's effluent has little effect, if any, on the distribution of fish in the local bays.

There was an obvious difference in the total population of fishes, shrimp, and crabs at different localities in the ship channel and a significant difference in the species comprising fish populations (Table 11). In general, there was a decrease, both in the number of species and in the total population of fishes, from lower to upper channel, as shown by the results of progressive trawl samples up the channel. During the period between March and July, fish were taken in only one of thirteen trawls in the upper channel region (Station 137) as compared to 6 of the 16 trawls in the middle channel region (Station III) and 15 of the 16 trawls in the lower channel region (Station VII). The principal reason for these differences may have been the lack of adequate dissolved oxygen to support fish life in the upper channel. It was found that when the surface dissolved oxygen content was 4.0 ppm or above, fish were usually taken in the trawls.

The difference in species composition between the lower and middle regions of the channel was due largely to the presence of high salinity fishes in the lower region such as *G. felis, C. arenarius, S. ocellata, P. octonemus, T. lepturus,* and *Prionotus sp.* Although the salinity was often higher in the lower region (Station VII) than at the middle region (Station III), on a number of occasions species differences were found when the chlorinity was about the same at Station III and Station VII. The difference in species composition probably results from factors such as the reduced dissolved oxygen at Station III.

A resident population cannot be maintained in the middle region of the channel (Station III) because of environmental conditions. The fish taken here are transient populations that move in and out of the area as the environmental conditions fluctuate. Wide fluctations of D.O. occur seasonally, daily, and hourly.

The per cent of the catch for certain species of fish in the middle region of the channel was quite different from the bays and usually from the lower region as shown by the Data in Table 12. The per cent of the catch data shown in Table 12 and the dissolved oxygen content data for these days indicate that the dissolved oxygen requirements of *M. undulatus* are higher than *L. xanthurus,* and that menhaden prefer water containing more than 4.0 ppm D.O. The species representation in the bays and channel (Station VII), the first date of appearance of marine fishes, and the last for fresh water fishes

TABLE 11

Comparison of trawl collections in the ship channel. Figures are the number of fish or crabs caught per trawl (c/t)

Date	Upper region Station 137		Middle region Station III		Lower region Station VII		Number of species	
	Crab c/t	Fish c/t	Crab c/t	Fish c/t	Crab c/t	Fish c/t	Same	Different
March 20	0	0	0	0	8	33	....	....
27	0	0	0	0	9	15	....	....
April 2	0	0	3	0	2	124	....	....
10	0	0	0	0	29	0	....	....
24	0	0	3	1	16	40	....	1
May 2	0	0	1	70	5	50	2	4
8	1	27	3	311	12	276	3	4
15	0	0	7	38	14	220	4	4
22	0	0	0	0	14	313	....	....
28	0	0	0	0	34	830	....	....
June 5	0	0	0	0	27	271	....	....
12	0	0	15	21	28	333	3	3
July 2	....	....	1	1	99	269	....	1
10	....	....	0	0	15	474	....	....
17	....	....	1	0	10	137	....	....
31	....	....	0	0	18	367	....	....

TABLE 12

Variation in percent of catch for certain species in the bays and channel

Date	Station	*Brevoortia sp.* including B. *patronus*	*Leiostomus xanthurus* percent	*Micropogon undulatus* percent	*Galeichthys felis* percent	Others percent	All fish catch per trawl
May 2	III	0	87	17	0	0	70
	VII	10	26	52	2	10	50
May 8*	III	1	82	17	0	0	311
	VII	1	85	12	0	2	276
	6–7	0.3	0.3	98	0	1	648
May 15	III	8	71	18	0	3	38
	VII	19	39	36	0.4	6	220
	4–5	2	2	84	0.26	13	386
	6–7	1	1	58	0	38	66
	8	13	1	72	0	12	282
June 12	III	48	52	0	0	0	21
	VII	78	9	13	0.3	0.9	333
	4–5	34	32	23	0	12	197
	8	4	22	62	0	12	94

* Station 137, *L. xanthurus*, 96%; *M. undulatus*, 4%.

between March 20, 1958, through July 31, 1958, are shown below. Certain species were not included as they occurred at all stations over the entire period.

Species	Marine or Fresh water	Present in Bay, Channel Or Both	Date of Appearance at Station VII	Date of Appearance at Bay Stations
Brevoortia sp.	M	both	April 2	April 2
G. felis	M	both	March 20	April 24
B. marina	M	channel	July 10	----------
C. faber	M	channel	July 31	----------
C. arenarius	M	both	June 5	April 24
T. lepturus	M	channel	May 15	----------
C. nebulosus	M	channel	June 26	----------
S. lanceolatus	M	channel	July 10	----------
A. grunniens	F	bay	----------	July 10
L. rhomboides	M	both	June 26	July 2
S. ocellata	M	channel	May 8	----------
L. productus and *L. platostomus*	F	bay	----------	March 20
A. mitchilli	M	both	May 2	April 2
P. octonemus	M	channel	May 15	----------

Most marine fishes migrating into the area in the spring and early summer were taken first at Station VII, the most seaward station, and some have been taken only at that station. Several of the marine fishes, however, were taken first in the bays due to immigration of the species between sampling periods.

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Some Opisthobranchs from the Northwestern Gulf of Mexico

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Abstract

A collection of marine slugs from the Northwestern Gulf of Mexico is described. Three of the eight species are new. All of the species have an affinity with warm water fauna.

Introduction

The Opisthobranchs described in this paper were collected along the Texas and Louisiana coasts principally by Professor Joel W. Hedgpeth, now Director of the Pacific Marine Station, Dillon Beach, California. Dr. Hedgpeth added expressive color sketches drawn from life. The specimens are kept at the Department of Zoology, University of São Paulo (P.O. Box 6994), São Paulo, Brazil.

Order Anaspidea

Aplysia donca, spec. nov. (Figures 1–5)

Occurrence: Texas, Mustang Island, Port Aransas, in a tide pool in sand, March 9, 1947; one specimen.

Description: The preserved animal is 65 mm long, 30 mm high, and 20 mm broad. It is soft, hence it must have been preserved in a well relaxed state. Alive it was "smoky black" (Dr. Hedgpeth), and is now uniformly greyish brown; in the wrinkles the color is a little denser and therefore darker, and slightly lighter on the sole. The inner margins of the parapodia and the gill (b) are dark; the rest of the mantle cavity is a little lighter. Seminal groove (d) and penis are white.

The tentacles form the ends of the buccal veil and bear a short furrow on the outside. Also, the very short rhinophores are grooved. The sole is narrow, 8–10 mm broad, smooth, without sucking disc. The short tail is rounded at the end; the foot (f) projects about 5 mm beyond the parapodia which join at the base of the foot. The height of their concrescence is one mm. The parapodial edges (rw, ws,) are thin; in front they are separated by a distance of 8 mm.

The opening of the shell chamber, the mantle aperture (me), is very wide; in somewhat distorted condition it measures 12x5 mm. The shell (Figure 2) is thin and flat, 33 mm long, 24 mm broad, with a 14 mm long sinus. The calcareous layer was broken, a condition frequently found in preserved *Aplysia*. The anal siphon (ar) is of the usual type. The purple gland (we) was evidently recently emptied; it contains only a little brownish secretion. The opaline gland (oi) is a field of simple glands 10 mm long, 4 mm broad which open separately, with exception of the foremost ones, whose ducts are united.

The central nervous system is similar to that of *Aplysia dactylomela* (MacFarland, 1909, Plate 2) in that the pleural ganglia are opposed to the pedal ones. The cerebral ganglia are almost confluent. The visceral loop, about 25 mm in length as in *Aplysia cervina* of comparable size, contains a complex of three joined but distinct ganglia. The largest, the abdominal ganglion, is in the middle; the parieto-supraintestinal ganglion of almost equal size lies to the right, and a smaller parieto-subintestinal ganglion to the left.

The jaws consist of tightly packed rodlets. The radula (Figure 4) has the formula 48x3-6.29.1.29.3-6. The rhachidian cusp is long and provided with several large basal denticles besides the small apical ones. Also the lateral teeth bear big secondary cusps, principally on the outside of the main cusp. The outermost teeth are rudimentary or have no cusps. The caecum (c) is slightly curved and its hind end shows on the dorsal surface of the digestive gland (1).

The reproductive organs are similar to those of *A. cervina* (E. and E. Marcus, 1959, Figure 9). The voluminous spermatheca is filled with sperm, indicating that the animal had copulated. The white penis (Figure 5) has a bulbar base and tapers distally. It bears slight longitudinal folds. The seminal groove (d) winds around its surface. The lining of the penial sheath is smooth.

Discussion of Aplysia donca: The present animal with sperm in its spermatheca is mature, though it is rather small; it has probably not attained the maximum size of the species. We have compared it principally with the species known from the Gulf of Mexico, the Caribbean, the American Pacific, the main Atlantic, and finally with those occurring elsewhere.

The systematic characters of our species are: parapodia joined at a low level posteriorly; large aperture of mantle; simple, multiporous opaline gland; shell flat, thin, without accessory plate; radula with long rhachidian cusp and elaborate but irregular denticulation of the lateral cusps; and penial sheath (praeputium of Engel and Eales' teminology, 1957, p. 85) smooth, without warts and spines.

A. willcoxi Heilprin, 1886 (Pilsbry, 1895, p. 80; Perry and Schwengel, 1955, p. 194), has some features in common with *donca*, for the radular teeth are similar (White, 1952, Figure 11), but its opaline gland opens by a single large orifice, and its mantle foramen is minute and tubular. Also, the other species listed from the Gulf of Mexico and the West Atlantic (Pilsbry, 1895, p. 75; Johnson, 1934, pp. 149–150) differ from the present one by characters other than color, with exception of the incompletely described *A. pilsbryi* (Letson, 1898, p. 193) from the northern coast of Yucatan which can be separated only by its color.

Pilsbry's list contains two or three synonyms of *A. brasiliana* Rang, 1828: *A. livida* d'Orbigny, 1837 (E. and E. Marcus, 1957, pp. 13–14); the little known *A. cailleti* Deshayes, 1857; and *A. guadeloupenis* Sowerby, 1869, which could as well belong to *A. dactylometa* Rang, 1828 (Eales, 1957a, p. 247). *A. schrammi* Deshayes, 1857, is a synonym of *A. dactylomela*. *A. cervina* Dall and Simpson, 1901, must be added to Pilsbry's list (for range see E. and E. Marcus, 1959, p. 3). Johnson mentions *A. protea* Rang, 1828, a synonym of *A. dactylomela*, and *A. floridensis* (Pilsbry, 1895) which can, at most, be maintained as a variety of *A. brasiliana* (Eales, 1957a, p. 246). The latter is now known from Mexico, and *A. cervina* is found at Charleston (Eales, 1957a). *A. (Tullia) juliana* Quoy and Gaimard, 1832, described as *A. badistes* Pilsbry, 1951, from Florida, must be added to Johnson's list.

A. morio Verrill, 1901 (Eales 1960, Bull. Brit. Mus. Nat. Hist. 5, p. 328–332) from Rhode Island to Florida and Texas, first recorded from Bermuda, is as soft as *donca*. Also the colour is similar. But the shell foramen is small in young specimens and closed in adult ones, the penis is curled round at the apex and without longitudinal folds. The radulae differ too.

The former marine connection between the Gulf of Mexico and the American Pacific coast was considered in the description of the originally Antillean *A. parvula* Mörch, 1863, from the Gulf of California (MacFarland, 1924, pp. 398–399). Among the American Pacific species *A. californica* Cooper, 1863, has parapodia joined low posteriorly and a radula not unlike that of *donca,* but its shell has an accessory plate, and its opaline gland is compound and uniporous. From Pilsbry's list of this region (1895, pp. 84–85) comprising species of *Aplysia* that occur from Dillon Beach to Peru, *A. rangiana* d'Orbigny, 1837, is a synonym of *A. juliana; A. panamensis* (Pilsbry, 1895) and probably also *A. chierchiana* Mazzarelli and Zuccardi, 1889, belong to *A. dactylomela*. More recently described species are *A. cedroensis* Bartsch and Rehder, 1939, and *A. vaccaria* Winkler, 1955, both belonging to the subgenus *Tullia* (Engel and Eales, 1957, p. 112); *A. nettiae* Winkler, 1959, is little different from *A. californica.*

Of the species occurring abroad, the radula of *Aplysia depilans* Linné, 1767, attracted our attention, but this is a *Tullia* with spiny warts on the penial sheath. *A. winneba* Eales (1957b, p. 180), also with a somewhat similar radula, has a small tube as mantle foramen, compound uniporous opaline gland, and characteristically fringed edges of the parapodia. The South African and Western Indic *A. maculata* Rang, 1828 (Macnae, 1955, p. 231), has a rather similar radula, but its tiny mantle aperture, and the course of the seminal groove along one and the same side of the penis, separate this quite differently colored species from *donca*.

Order Notaspidea

Pleurobranchaea hedgpethi Abbott, 1952 (Figure 6)

Occurrence: Texas, Port Isabel Channel, March 21, 1947; one specimen. Further distribution: Bay of Campeche, 62–66 mm; Texas, Port Aransas (type locality), in shallow water over muddy bottom.

Description: The present animal is preserved 45 mm long and 26 mm broad, hence bigger than the types. In life, the slugs are sepia brown with lighter mottlings (Abbott, 1952, p. 2), the present preserved specimen has light papillae standing out from the brownish skin. The small, firm, dorsal spur close to the hind end of the foot is black. The pedal gland on the ventral side is 10 mm long.

The radula comprises 36 rows with 56 teeth in each half row. The ctenidium has 26 pairs of pinnules (secondary lamellae of Abbott's terminology), with about 35 leaflets each. The branchial membrane extends to about the 13th pinnule. As the posterior pinnules are much shorter than the anterior ones, Abbott's indication of the attachment of the gill along most of its length is correct. The anus lies over the seventh pinnule, while it is farther behind in Verrill's species *P. tarda* and *obesa* (Bergh, 1897, pp. 31, 35), and in *P. morosa* and *agassizii* (Bergh, 1892, p. 28; 1897, p. 48).

In our discussion of *P. hamva* (E. and E. Marcus, 1957), we separated this species from *P. hedgpethi* by its dorsally directed, tongue-like extension of the membrane that surrounds the genital apertures (p. 26). In *P. hedgpethi,* it points forwards. Moreover,

there are 38 rows with 60 teeth in the half row in the radula of *P. hamva*, whose biggest preserved specimens are only 33 mm long. The only 19 mm long *P. inconspicua* Bergh (1897, p. 49) has 34 rows with up to 72 teeth in the half row. In this species the caudal spur is red.

The border of the frontal veil, minutely serrated in *P. hedgpethi*, tuberculated in *P. hamva* and *inconspicua*, is not specifically different, but varies with contraction. The spermatheca of the present specimen (Figure 6,s) is globular as in *P. hamva*, in Abbott's it is much longer than broad. In his figure (Plate 1, Figure 7) the bifurcation of the spermoviduct is not evident.

The Western Atlantic species of *Pleurobranchaea* can be arranged in the following key:

1. Gill free for half or more of its length 2
   Gill free for less than half of its length 4
2. Gill with 15 pairs of pinnules ..... *morosa* (Bergh, 1892)
   Gill with 27–32 pairs of pinnules 3
3. Eighty teeth in the radular half row of a 75 mm long preserved specimen ..... *obesa* (Verrill, 1882)
   Ninety teeth in the half row of a 20 mm preserved slug ..... *agassizii* Bergh, 1897
4. Tail with dorsal spur 5
   Tail without spur ..... *tarda* Verrill, 1880, with an Antillean variety (Bergh, 1897)
5. Border of genital aperture with dorsal flap 6
   Without genital flap ..... *meckelii* var. *occidentalis* Bergh, 1897
6. Flap pointing forwards ..... *hedgpethi* Abbott, 1952
   Flap pointing upwards 7
7. Caudal spur red ..... *inconspicua* Bergh, 1897
   Caudal spur black ..... *hamva* E. and E. Marcus, 1957

For our list of 18 species and varieties of *Pleurobranchaea* (E. and E. Marcus, 1957, pp. 25–27) the description of *P. algoensis* Thiele (1925, p. 282) from South Africa was not available. Now we have it, but can only separate *algoensis* from two other South African species by its spur. In his description of *P. japonica*, Thiele (1925, p. 283, Plate 45, Figure 8) used the aspect of the mouth as a specific character. However, we consider this character unreliable since it depends too much on protraction or retraction of the muzzle to be a reliable systematic character.

Order Nudibranchia, Suborder Doridacea Cryptobranchia

Discodoris hedgpethi, spec. nov. (Figures 7–11)

Occurrence: Texas, Port Aransas, October 12, 1948; three specimens.

Description: The animals preserved are up to 45 mm long, 22 mm broad, and 10 mm high. One of the living specimens was 110 mm long, 66 mm broad, and 10 mm high. The color, "but slightly faded" (Dr. Hedgpeth) from the living state, is pale olive green with black spots and blotches, up to 3 mm in diameter; the sole of the foot is less spotted. A superficial net of melanophores leaves small epidermal papillae free; other groups extend from the upper connective tissue far inwards. The papillae, 0.15–0.3 mm in diameter, are stiffened by a few convergent spicules 0.4 mm long, and end with blunt

summits. The foot is 30 mm long, 12 mm broad, bilabiate and notched in front, and undulate on the sides.

The conical tentacles are not grooved. The rhinophores stand 4 mm apart from one another and from the anterior border; the rims of the rhinophorial grooves are beset with papillae of the common type. The perfoliation consists of about 25 leaflets on either side. The rhinophores and the six 3 and 4-pinnate gills (b) are slightly pigmented. The 5 mm broad branchial groove lies about 10 mm in front of the hind end.

The central nervous system (ce) is wrapped in a strong, tough, transparent capsule of connective tissue. The surface of the central nervous mass is smooth, not nodular as is sometimes reported for species of *Discodoris* (Bergh, 1884, p. 94; Risbec, 1956, Figure 47). The ganglia are indistinctly separated, the cerebropleural ganglia are medial, and the pedal ganglia lateral. The visceral loop and the long pedal and parapedal commissures run within a common sheath of connective tissue. A thickening with many ganglionic cells at the right foot of the visceral loop is the abdominal ganglion, and some nerve cells also occur in the thinner left root. A medial nerve goes out from the abdominal ganglion. This nerve contains two cells which evidently correspond to the genital ganglion of *Austrodoris macmurdensis* (Odhner, 1934, Figure 27, G). Rhinophorial or olfactory ganglia are present; the eyes are sessile and widely spaced. Especially the pleural ganglia contain nerve cells whose nuclei are up to 160 micra in diameter.

Scattered single melanophores occur in the peritoneum. The lips bear two triangular areas of stratified rodlets up to 150 micra long, and six micra thick. The radula comprises 26 rows of 44.0.44 teeth. All are simple hooks with the exception of the innermost ones whose cusps are provided with a denticle (Figure 9). These and the outermost teeth are shorter than the others. The symmetrical salivary glands are long straps. The 9 mm long and 1 mm wide oesophagus (oe) enters the middle of the left wall of the stomach (oo). The latter lies free; at its hind end the fundus of the caecum (c) projects from the liver (l). From its anterior end the intestine (i) curves to the right and backwards. Under the rectum lies the pyriform reno-pericardial communication (rc). The anus (ar) is located a little behind the centre of the branchial circle.

From the hermaphrodite gland a long, thin, and straight hermaphrodite duct (er) leads to the ampulla (a), a winding tube whose end bifurcates into the male and female ducts. The first enters a compact prostate (q) and leaves it as a long muscular efferent duct (d). This ends with a pleurembolic penis (p) armed with cuticular spines (Figure 11) and lodged in a spacious male atrium (am). The outer opening (ae) is in common for the male atrium, the nidamental duct (ni), and the vagina (v).

The inner oviduct (o) enters the female gland mass (g). The long and wide vagina (v) runs above the nidamental duct (ni). The epithelium of its inner part is thrown into numerous transverse folds. The enormous spermatheca (s) is filled with sperm and dark particles. The fertilizing duct (e) begins immediately beside the entrance of the vagina and communicates with a small pear-shaped spermatocyst (sc) in its inner third. It joins the gland mass (g) near the inner oviduct (o).

The species is named for Professor Dr. Joel W. Hedgpeth, Director of the Pacific Marine Station, Dillon Beach, California.

The holotype is a preserved specimen, 45 mm long.

Discussion of Discodoris hedgpethi: Most species of *Discodoris* live in the Indo-West Pacific, while only seven were described from the American Altantic coasts (Bergh, 1877, pp. 530–534; MacFarland, 1909, pp. 66–82; White, 1952, p. 113; Marcus, 1955,

pp. 143–151). Of these only *D. branneri* MacFarland and *D. evelinae* Marcus with armed penis must be compared with *D. hedgpethi*. *D. muta* Bergh, whose penis was not described, has a yellowish white sole without dark spots; its labial rodlets are up to 100 micra long.

There are 72–80 teeth in the half row of the radula in *evelinae*, whose body size is the same as that of *hedgpethi*. The dark blotches of *evelinae* appear checkered by the longitudinal and transverse fibres of the cutaneous muscles. *D. branneri* from Northeastern Brazil, Alagoas, more closely approaches *D. hedgpethi* than *evelinae* from the coast of S. Paulo. Its oesophagus is short and wide, 3 mm long by 1.5 in diameter, and enters the stomach from the front. Its much smaller spermatheca (MacFarland, 1909. Figure 65, spth) may be less distended than in the specimen of *hedgpethi* examined. The shorter conical penis, the "glans" of MacFarland's terminology (p. 70, Figure 65, p), and its spines of equal length and diameter (Figure 64) are specific. The peculiar broadened cusp of the innermost radular teeth of *hedgpethi* was not noted for *branneri*, and the labial rodlets of the latter attain a maximum length of 96 micra against 150 in *hedgpethi*.

Only the three geographically neighboring species, *branneri*, *evelinae*, and *hedgpethi*, have a penial armature, contrary to the type (Bergh, 1877, p. 519) and the diagnosis of the genus. But the state of our knowledge does not yet recommend their subgeneric or generic separation. Some species, e.g., *D. notha* (Bergh, 1877, pp. 530, 532), have a thin penial cuticle, and for many others the penis is not described.

The autotomy of pieces of the notal brim reported by the collector for the present species is frequent in slugs of *Discodoris* (Marcus, 1955, p. 143) and led Risbec (1956, p. 15) to name a *Discordoris*, *D. notiperda*.

Order Nudibranchia, Suborder Doridacea Phanerobranchia

Corambella barataríae Harry 1953 (Figures 12–13)

Occurrence: Texas, Port Aransas, on *Sargassum* in August, 1947; April, 1948; and February, 1949 together with two polyclads, *Gnesioceros floridana* Pearse, 1938); a total of nine slugs. Grand Isle, Louisiana, December 9, 1949; Mr. Dan A. Wray collected 12 specimens.

The first material of this species was collected in summer, fall, and winter on the oyster beds of lower Barataria Bay, Grand Isle, La., and fully described by Harry (1953). We give a figure of the situs viscerum and the reproductive organs to complete the description (Figure 7–11).

Description: Male and female follicles of the hermaphrodite gland (h) are separated, as Harry indicated (p. 6), but an exclusive terminal location of the male acini was not noted. The glandular part of the oviduct begins as an eosinophilous albumen gland (aa), in the animal on the left side, and passes to a cyanophilous mucus gland (ms) on the right side. The 0.3 mm long penis (p), transversely drawn in the diagram, actually extends in antero-posterior direction. Some additions to the first description can be given: the wide female atrium (mw) has glandular walls. The insemination duct (e) leaves the spermatheca (s) far from the entrance of the vagina (v) into the latter and begins with a sphincter (zi). The spermatocyst (sc) is intercalary in the insemination duct. The opening of the latter into the albumen gland lies near that of the inner oviduct (o). In our specimen spermatheca (s) and ampulla (a) are of different size,

while Harry (p. 7) found the spermatheca about as large as the seminal vesicle, i.e., the ampulla. This is due to different degrees of filling and is morphologically insignificant.

The minute penis and the topographic relations between albumen gland, mucus gland, and insemination duct distinguish the reproductive organs of *C. carambola* Marcus (1955, Figure 217) from those of *C. baratariae*. Further differences are: the rounded (*baratariae*, Figure 12, f) and pointed (*carambola*) hind end of the foot; three (*b.*) and two (*c.*) pairs of branchial glands (ei); and the shape of the five outer lateral teeth of the radula. The color pattern is less different than it appears from the comparison of the light *baratariae* (Figure 1) with the dark *carambola* (Figure 209). The present material also contains rather densely pigmented specimens.

Harry (p. 1) follows MacFarland and O'Donoghue (1929, p. 2) preserving the family name Hypobranchiaeidae used by Fischer (1887, p. 530). But the 15 cm long *Hypobranchiaea fusca* A. Adams, 1847, from the Yellow Sea, is systematically quite uncertain. On the other hand, *Doridella obscura* Verrill, 1870, certainly belongs to the Corambidae. This species recorded from Vineyard Sound to Great Egg Harbor, N. J. (Johnson, 1934, p. 158), ought to be re-examined. Probably *Corambella depressa* Balch, 1899, from Long Island, Cold Spring Harbor, will prove to be identical with it. In that case *Corambella baratariae* and *C. carambola* must be called *Doridella*, but the family name can remain Corambidae, though *Corambe* is from 1871.

Order Nudibranchia, Suborder Eolidacea, Family Favorinidae

Cratena kaoruae Marcus, 1957 (Figure 14)

Occurrence: Texas, Port Isabel Channel, and Harbor Island, Port Aransas, March 15 and 18, 1948; 11 specimens. Louisiana, Grand Isle, December 9, 1949; Mr. Dan A. Wray collected one specimen. Further distribution: Cananéia, 200 km southwest of Santos (Brazil), in a lagoon of variable salinity (14–26 ppt).

Description: With the present rich material we complete the description of the species based on three animals (Marcus, 1957, p. 472). Alive, the Texas specimens were brownish grey on the dorsal side with greenish-brown-grey hepatic diverticula in the cerata. The underside was white. The length of the biggest preserved specimens is 12 mm, breadth and height 5 mm, and longest cerata 4 mm.

The present specimens agree with the original material in having scattered low tubercles on the rhinophores. The cerata stand in nine groups in the largest animal. The four anterior ones are horseshoes, the five hinder ones rows; the innermost cerata are longest. The following numbers exemplify the distribution of the cerata: first arch, 14; second, 15; third, 13; and fourth, 12. The rows have 6,5,4,3, and 2 cerata.

The genital opening lies in or under the first arch, the renal pore in the interhepatic space, and the anus within the second arch. The surface of the liver diverticula in the cerata is nodulose.

The jaws correspond to the first description; the denticles of the masticatory border (l.c., Figure 221) end with minute spines. The radula of a 9 mm long animal consists of 17 teeth with three to six denticles on either side of the median cusp. The length of the lateral denticles varies somewhat after the view and may appear a little longer than in the first figure (Figure 222).

The reproductive organs have a long, winding ampulla (a) at whose end male and

female ducts separate. The male duct becomes prostatic (q) near its origin. This coiled part continues outwards to the penis (p) where the glands disappear (d). The big penial papilla is almost spherical and provided with a dorsal appendage (ze) at its base, which shows as a fold on the dorsal side of the evaginated penis.

The inner oviduct (o) is continuous with the insemination duct (e); a dilated portion between both these ducts might function as a fertilization chamber. The openings of insemination duct and vagina (v) into the spermatheca (s) are separate but neighboring. The fertilized eggs must pass through the vagina to enter the gland mass (g) drawn much smaller in the diagram than it is. Also, the alien sperms must pass through the outer oviduct or nidamental duct (ni) to reach the vagina and spermatheca. A common genital opening (ae) serves as an outlet for a glandular pouch, the female atrium (mw), and the male atrium (am).

We know from a letter of Dr. Henning Lemche, Copenhagen, of March 14, 1958, that he has proposed the suppression of *Cratena* Bergh, 1864 (in German: 1870) to the International Commission on Zoological Nomenclature. We cannot anticipate the decision of the Commission, and so we use *Cratena* as do Odhner (1944, p. 22) and Macnae (1954, p. 28), and in observance of article 29 of the Rules.

Order Nudibranchia, Suborder Eolidacea, Family Aeolidiidae

Spurilla neapolitana (Delle Chiaje, 1823) (Figure 15)

Occurrence: Texas, Port Aransas, June 25, 1948 and February 11, 1949; a total of four specimens. Further distribution: Mediterranean including the Adriatic; Atlantic coast of France, Arcachon; Morocco; Canary and Cape Verde Islands; Sargasso Sea; Florida, Miami area; and coast of Brazil, Alagoas, and S. Paulo.

Description: In a study of Florida opisthobranchs (Bull. Mar. Sci. of the Gulf and Caribbean, in press) we have given the reason for suppressing *braziliana* MacFarland (1909, p. 91) as species and as variety, and now we confirm this. The present material contains a preserved animal about 20 mm long, whose mandible is 5 mm long, while that of a 28 mm long specimen is 4 mm. The breadth of the denticles varies very much in neighboring radular teeth. It may be 3.2 micra in one tooth and 11 micra in the preceding or following one. On the same tooth the denticles are of rather equal size but in adjacent teeth a minimum of 47 and a maximum of 90 denticles may occur on either side of the middle.

The white spots on head, back and cerata characteristic of the species were also indicated by Dr. Hedgpeth, the collector of the present material.

Berghia coerulescens (Laurillard, 1830) (Figures 16–17)

Occurrence: Texas, Port Aransas, November 2, 1948; two specimens. Lydia Ann Channel, between the Gulf and Aransas Bay, July 22, 1946; one specimen. Further distribution: Mediterranean; Atlantic coast of Morocco and France, northward to the French Channel coast; West Indies, Tobago Island; coast of Brazil, S. Paulo.

Description: The preserved animals are 9.7 (Port Aransas), and 6 mm long. The color alive, "with scarlet trimmings" (Dr. Joel W. Hedgpeth), is in part preserved. Tentacles and rhinophores are of about the same size, the antero-lateral angles of the foot are somewhat shorter. The posterior surface of the rhinophores (Figure 17) bears

tubercles which form more or less distinct rows; the anterior surface is smooth. The cerata stand in five arches followed by three rows. The genital aperture lies at the beginning of the first horseshoe, the anus within the second.

This well-known and recently re-described species (Marcus, 1957, p. 477) does not need a new description. To the recently listed species (Marcus, 1958, p. 68) *Berghia dela* Marcus from the Maldive Islands was added (Abh. Akad. Wiss. Mainz, 1960). Its rhinophores bear tubercles over its entire outer surface. The same applies to *B. japonica* (Baba, 1933), *B. amakusana* (Baba, 1937), and *B. norvegica* Odhner, 1939. *Berghia fusiformis* (Baba, 1949) has tubercles only on the posterior side of the rhinophores as *coerulescens*, but all its liver branches form rows, not arches. In the doubtful *B. modesta* Trinchese, 1882, the posterior tubercles diminish in size on the sides of the rhinophore and pass on to the front where they leave a vertical line free (Pruvot-Fol, 1954, p. 435).

Cerberilla tanna, spec. nov. (Figures 18–19)

Occurrence: Texas, off Sabine Jetties, 3,6–12 m, June 15, 1951; Dr. H. H. Hildebrand collected one specimen.

Description: The strongly contracted and curled animal is about 15 mm long with an about 6 mm broad sole. The longest cerata are 7–8 mm long. The color of the preserved specimen is dirty yellow with an orange-brown spot on the outer surface of many, not all, cerata under the cnidosac.

The tentacles (t) are very long, about 6 mm, and end with a fine point. The rhinophores (r) are minute, 1 mm long, and perfoliated. The anterior border of the foot is simple, the antero-lateral corners (oc) are produced and pointed but short. The sides of the foot bear a wavy brim. The tail is short.

The firm cerata stand in about 13 quite straight rows and leave a dorso-median line free. The anterior rows contain only short cerata. The longest cerata are those nearest the mid line and in the middle of the animal. These middle rows also contain the greatest number of cerata, *viz.*, 10–11. The anterior side of the cerata bears a small basal outgrowth into which the hepatic diverticulum does not enter. The cnidosacs are short, about 0.4 mm in length.

The gonopore lies under the third row; the anus under the sixth.

The brown jaws are about 2.5 mm long; their hinge is similar to that of *Spurilla neapolitana*. The border of the masticatory process is smooth. The 2 mm long radula comprises 15 rows, the hindmost of which is only primordial. The tooth is 0.4 mm broad. The outermost denticles are longest, the others smaller and of unequal size. There are six to eight bigger denticles on either side of the tooth and generally one to three smaller ones stand between two of the bigger denticles. Of the three smaller ones, that one in the middle is usually a little longer than the two others. All denticles insert on the common base, while in most species of the genus the smaller ones sit on the higher ones. In the middle of the tooth there are four to seven small denticles of different size, the median of which is minute.

In order to keep this zoogeographically remarkable animal as intact as possible no further inner organs were dissected.

Discussion of Cerberilla tanna: The radula is the best character for the distinction of the new species from the previously described ones (Pruvot-Fol, 1934, p. 52). To these *C. asamusiensis* Baba (1940, p. 108) was added. In all older species some of the sec-

ondary denticles originate on the primary ones with exception of *C. ambonensis* Bergh (1905, p. 225). In the latter the small denticles insert between the longer ones as in *C. tanna*, but the outermost denticles are smaller than the two following inwards. Furthermore, primary and secondary denticles do not alternate so regularly in *ambonensis* (Plate 19, Figure 33) as in *tanna*. The antero-lateral corners of the foot are longer in *ambonensis* (Plate 5, Figure 6; living specimen) than in *tanna*, even under consideration of their shortening in the preserved specimen. Their length in living *tanna* is probably similar to that of *asamusiensis*.

The genus *Fenrisia* Bergh, 1888, is a synonym of *Cerberilla* Bergh, 1873 (Pruvot-Fol, 1934, pp. 54–55, 81: addendum III).

Faunistic Notes

The material comes from a region whose opisthobranch fauna is very little known (Hedgpeth, 1953, p. 198); accordingly three out of eight species are new, and, furthermore, three have been published only in the last decade. Of the new species, *Aplysia donca* bears no special relationship to forms in other regions; its radula is what Eales calls "the common type of radula in tropical Aplysias" (1957b, p. 183). The new *Discodoris* is closely related to two species from the Brazilian coast. The new *Cerberilla* is the first Atlantic representative described of an Indo-West Pacific genus, principally, but not exclusively, from warm waters.

Cratena kaoruae was first found in a lagoon in southern Middle Brazil. It seems to be an estuarine species, and for such species wide distribution is frequent (Hedgpeth, 1953, p. 206). *Pleurobranchaea hedgpethi* is related to the Brazilian *P. inconspicua* and *P. hamva*. Whether *Corambella baratariae* is nearer to the South or the North American *Corambella* cannot be decided, as the latter is imperfectly known. A further complication is that *Corambe batava* Kerbert, 1886 (Van Benthem Jutting, 1922, p. 400), from the Netherlands, seems to be a *Corambella* (Engel, 1936, p. 106).

The two remaining species, *Spurilla neapolitana* and *Berghia coerulescens*, occur on both sides of the Atlantic in warm and warm-temperate waters.

The present collection has the characteristics of a warm water fauna.

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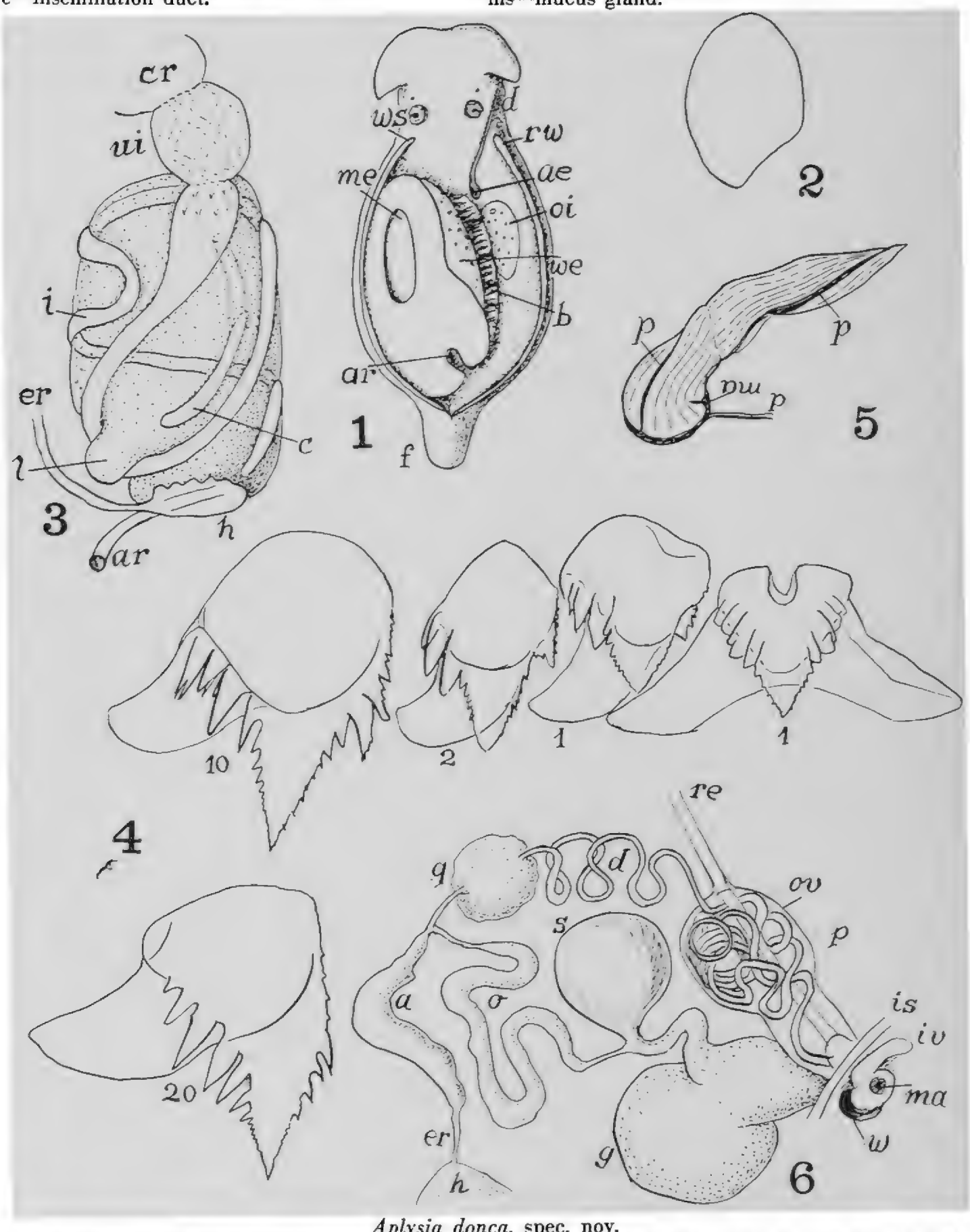
Explanation of Abbreviations Used in Figures 1–19

a—ampulla.
aa—albumen gland.
ae—genital aperture.
ai—glands of oral tube.
am—male atrium.
ar—anus.
b—gill.
c—caecum.
ce—cerebral ganglion.
co—heart.
cr—crop.
d—efferent duct or seminal grove.
e—insemination duct.
ea—blood glands.
ei—branchial glands.
er—hermaphrodite duct.
f—foot.
g—female gland mass.
h—hermaphrodite gland.
i—intestine.
is—body wall.
iv—flap of genital opening.
l—digestive gland.
ma—male aperture.
me—mantle aperture.
ms—mucus gland.



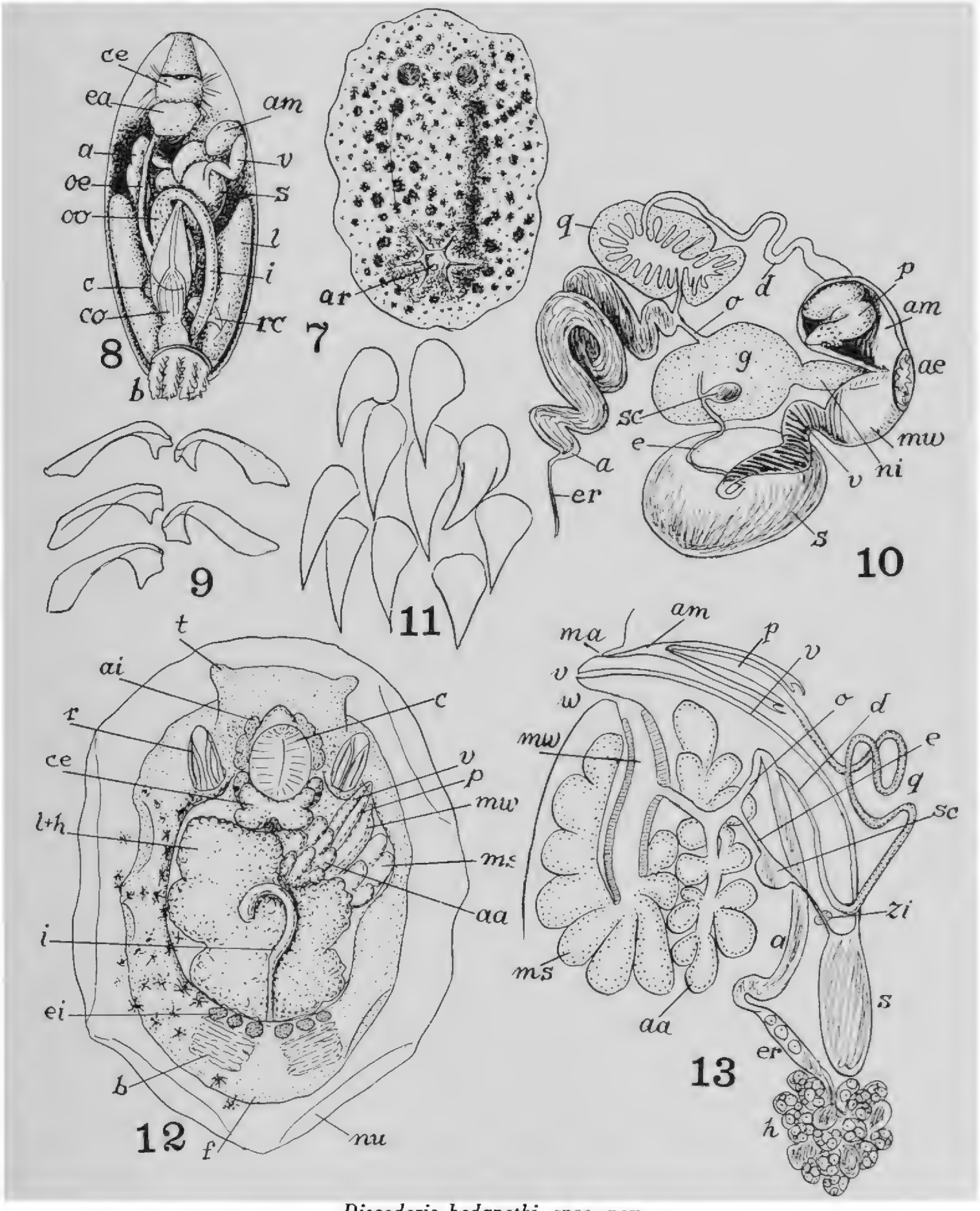
Aplysia donca, spec. nov.

FIG. 1. Diagram of dorsal aspect with removed parapodia. FIG. 2. Shell. FIG. 3. Gut. FIG. 4. Radular teeth. FIG. 5. Penis.

Pleurobranchaet hedgpethi Abbott

FIG. 6. Diagram of reproductive organs.

mw—female atrium.
ni—nidamental duct.
nu—notum.
o—oviduct.
oc—foot corner.
oe—oesophagus.
oi—opaline gland.
oo—stomach.
ov—muscle sac.
p—penis.
q—prostate.
r—rhinophore.
rc—renopericardial duct.
re—retractor.
rw—right parapodium.
s—spermatheca.
sc—spermatocyst.
t—tentacle.
ui—gizzard.
v—vagina.
w—female aperture.
we—purple gland.
ws—left parapodium.
ze—dorsal flap of penis.
zi—sphincter.

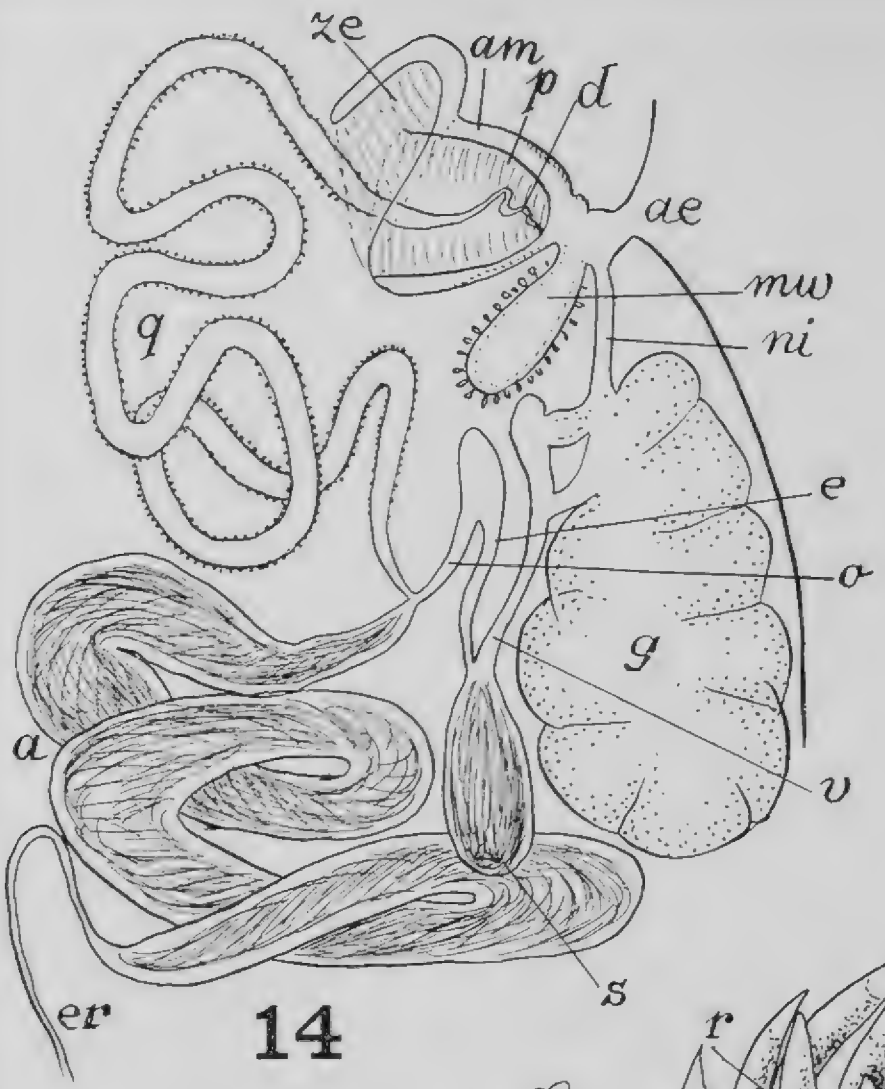


Discodoris hedgpethi, spec. nov.

FIG. 7. Dorsal view of preserved slug. FIG. 8. Situs viscerum. FIG. 9. Innermost teeth of radula. FIG. 10. Diagram of reproductive organs. FIG. 11. Penial spines.

Corambella baratariae Harry

FIG. 12. Situs viscerum in clarified slug. FIG. 13. Diagram of reproductive organs.



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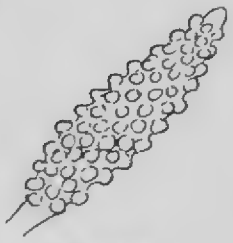

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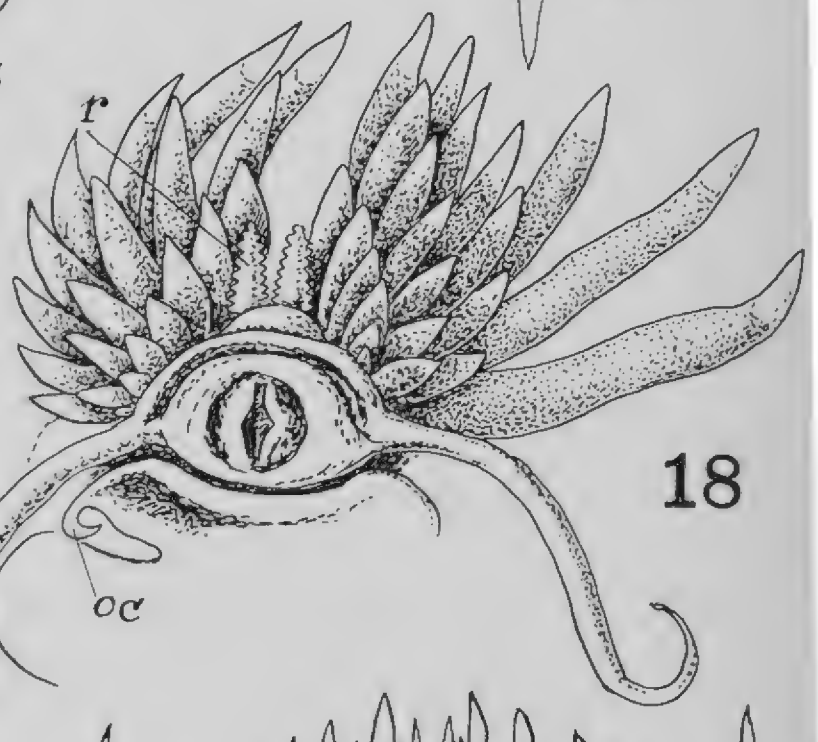

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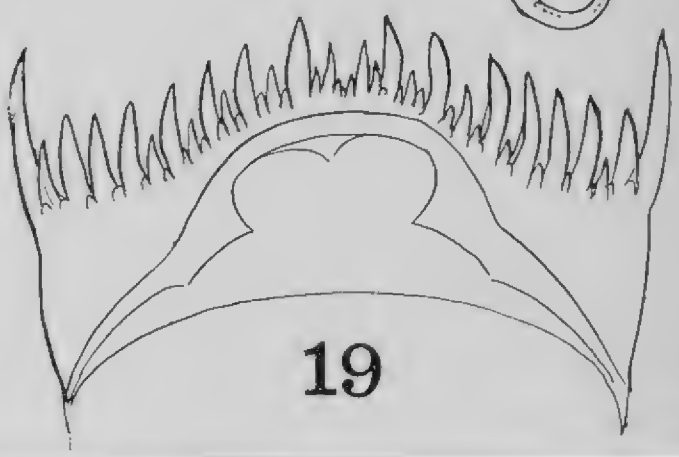

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Cratena kaoruae Marcus
FIG. 14. Diagram of reproductive organs.

Spurilla neapolitana (Delle Chiaje)
FIG. 15. Dorsal view of living slug, from a colored sketch by Dr. Joel W. Hedgpeth.

Berghia coerulescens (Laurillard)
FIG. 16. Dorsal view of living slug, from a colored sketch by Dr. Joel W. Hedgpeth; the red marks given in black. FIG. 17. Posterior view of rhinophore.

Cerberilla tanna, spec. nov.
FIG. 18. Fore end of preserved slug. FIG. 19. Radular tooth.

A Collection of Marine Algae from the Chandeleur Islands

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Abstract

Thirty-five species of marine algae were collected among the Chandeleur Islands, northern Gulf of Mexico. Ecological and phytogeographic relations of these algae are discussed and an annotated list of species is included. Most of the tropical elements of the Chandeleur Island flora were absent from the Ship Island flora (Mississippi Sound). It is suggested that the absence of many of these species from the Ship Island flora is not an accident of dispersal, but rather a failure of establishment and survival.

Introduction

In March and August of 1954 collections of marine algae were made in connection with studies of the ecology of marine invertebrate animals of the Chandeleur Islands, northern Gulf of Mexico. Since little is known about the distribution and ecology of the marine algae of this area (Taylor, 1954; Humm and Caylor, 1957), the results of the work on the algae are treated here separately from the invertebrate study.

Grateful acknowledgment is made to the Commercial Seafood Division of the Louisiana Wildlife and Fisheries Commission for support of the field work and to Dr. Francis Drouet of New Mexico Highlands University for determination of the majority of the blue-green algae listed.

Location and Description of the Islands

The Chandeleur Islands make up the easternmost tip of the State of Louisiana and are located about 30 miles south of Biloxi, Mississippi, and about 15 miles south of Ship Island, Mississippi Sound. The Chandeleur chain consists of one main island and several smaller islands forming a narrow arc about 40 miles in length (Figure 1). This arc has a north south axis, is bowed toward the east, and in the protected western concavity are several other islands of various sizes. This entire series of islands lies on the eastern fringe of the modern Misissippi River delta.

Topographically, the Chandeleur group is made up of typical barrier islands as defined by Shepard (1952). The eastern front of the island chain is exposed to the open gulf and is characterized by breaking waves and shifting sands. Tall dunes border the beach, and behind these lie the low lands which account for most of the width of the

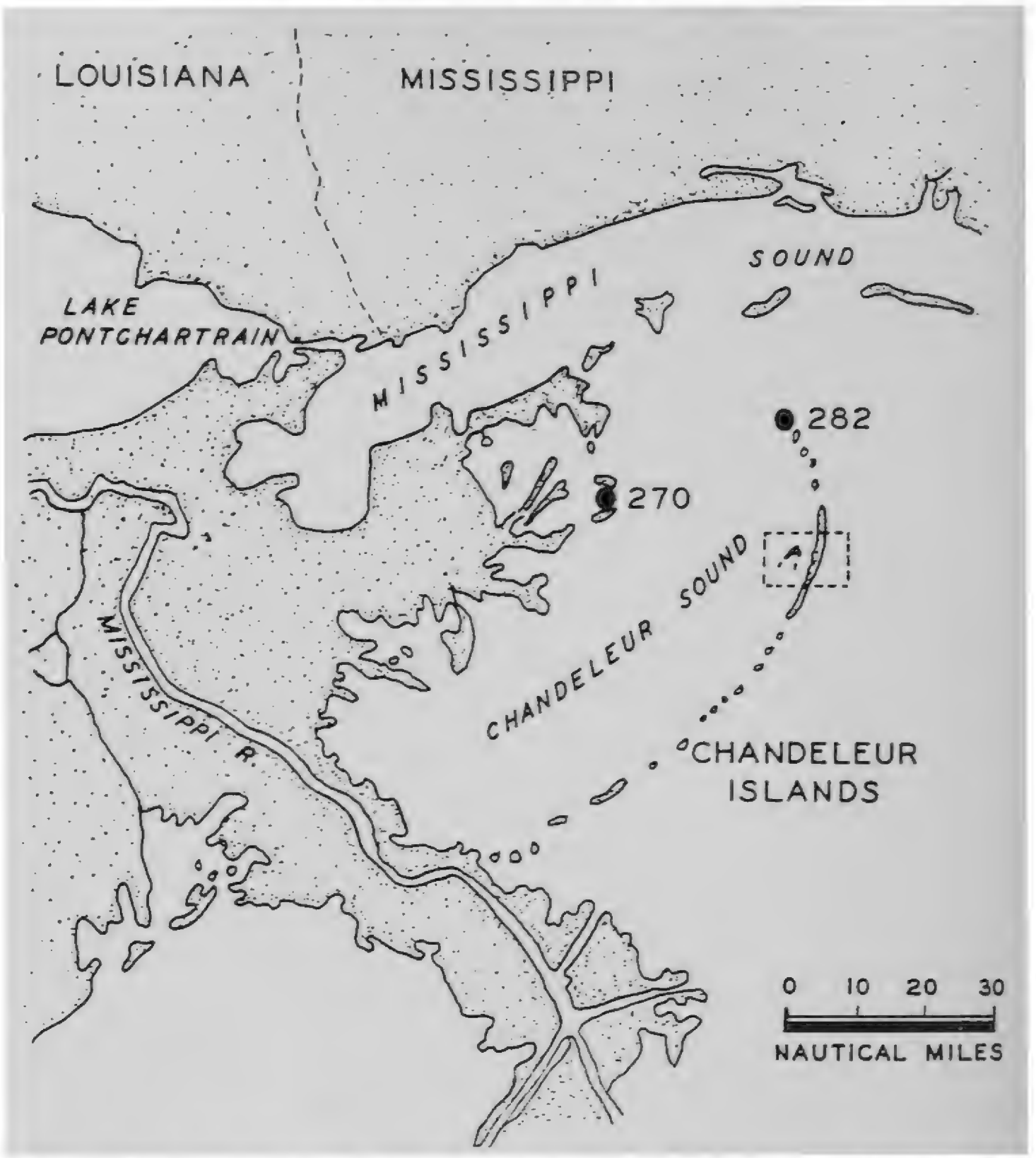

FIG. 1. The Chandeleur Islands, northern Gulf of Mexico, in relation to the Mississippi River mouth and delta and to Mississippi Sound. The small, rectangle of dotted lines indicates the area in which most of the collecting was done; it is enlarged in Figure 2. The locations of stations 270 and 282 are shown here as they are outside the area included in Figure 2.

islands. This area, only slightly above sea level. supports a dense growth of shrub-like mangroves and other hardy strand vegetation. The protected lee side of the islands is deeply dissected by a complex natural network of blind cuts, interconnecting tidal creeks, and occasional isolated ponds. At its western fringe the low land borders shallow, submerged flats which gradually deepen to a north-south channel (Smack Channel) paralleling the Chandeleur chain and separating these from other adjacent islands (Figure 2).

The western shores of the Chandeleur Islands support dense growths of emergent marsh vegetation. In the protected cuts and canals, and to some extent upon the flats behind the islands, are found "submarine meadows" consisting of at least three species of "sea grasses," *Thalassia testudinum* Konig, *Cymodocea manatorum* Ascherson, and

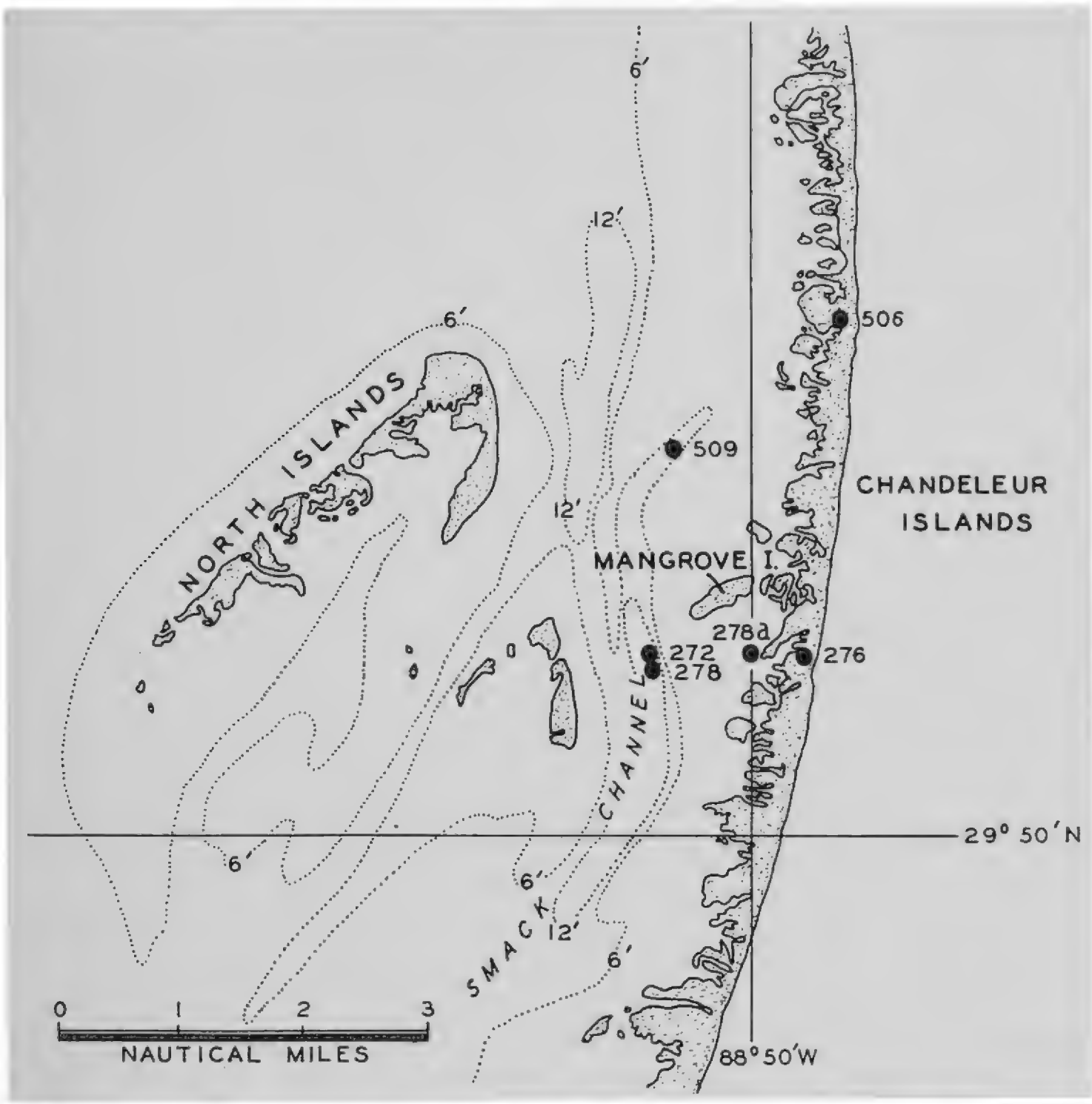

FIG. 2. An enlarged portion of the area among the Chandeleur Islands showing the location of most of the collecting stations and depth contours (see rectangular insert in Figure 1).

Diplanthera wrightii (Ascherson) Ascherson. *Halophila engelmannii* Ascherson and *H. baillonis* Ascherson probably occur in deeper water around the Chandeleurs. Because of the greater transparency of the water, both *Thalassia* and *Cymodocea* occur at greater depths among the Chandeleurs than they do in Mississippi Sound (Humm, 1956). These grass-like submarine flowering plants form the base for attachment of numerous algal species (Figure 3).

Field Data

Collections of algae were made during the months of March and August of 1954 from a variety of habitats on the protected (west) side of the islands, especially in the vicinity of Mangrove Island near the center of the chain. Habitats included an isolated pond (Station 276), shallow and deeper flats (Stations 506, 509), cuts and canals (Station 278), and deeper channels including Smack Channel (Station 272), and a deeper area at the north end of the island chain (Station 282). The substrata, for the most part, were

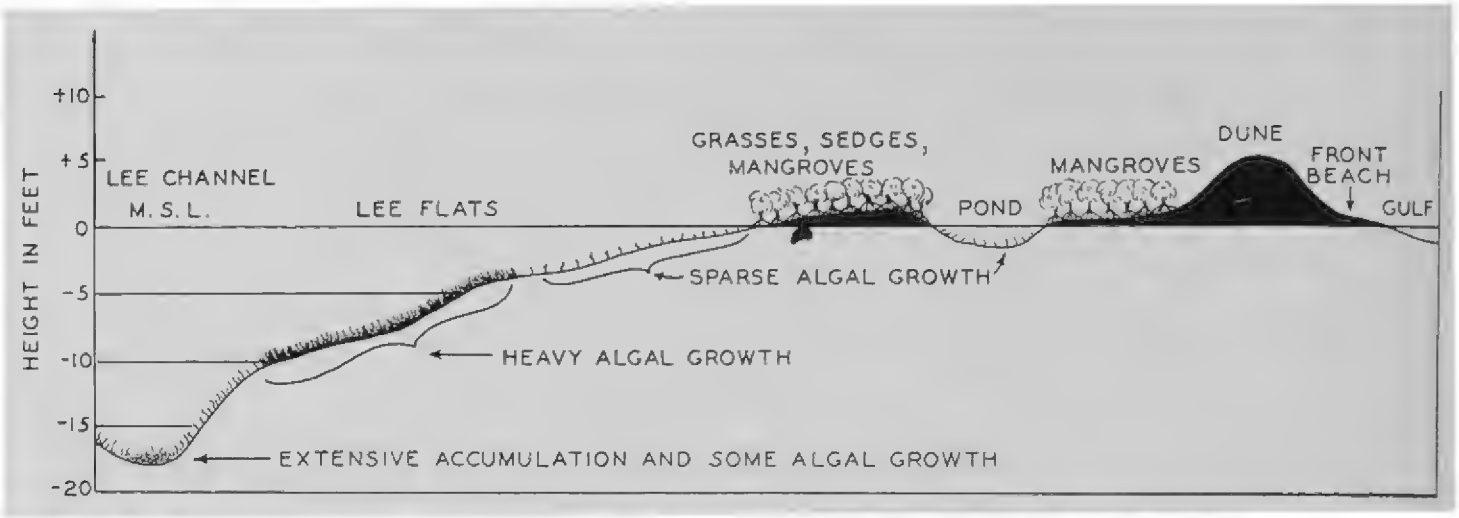

FIG. 3. A cross-section diagram of the Chandeleur Islands showing the relative abundance of algal growth at three depths and in an isolated pond. The distribution and abundance of sea grasses are not shown.

firm and composed of a mixture of mud and sand with various quantities of decaying marsh grasses, sea grasses, and algae on the surface of the bottom. Organic material tended to accumulate in troughs and basins and was especially rich in Smack Channel.

Water temperatures on March 27–29 ranged from 20–21°C. On August 25 and 26 they were 29–30°C. Salinity in March was 31–32 ppt, but in August was 32–40 ppt. The shoal waters surrounding the Chandeleur Islands are usually only slightly fresher than waters of the open gulf. Since the islands are some distance from shore, their surrounding waters are less subject to rapid fluctuations in temperature and salinity than inshore waters to the north and east (Mississippi Sound, for example). During the summer months a combination of heavy evaporation and poor circulation results in the development of hypersaline conditions in some of the cuts and canals of the islands, and accounts for the high August salinities recorded. There is a slow current through Smack Channel which, augmented by tidal currents, promotes some water exchange over the adjacent flats.

Collections were obtained by means of trawls and dredges. For this reason the presence of a particular algal species at a station does not necessarily mean that it grew there. Only sparse algal growth was observed in water shallower than four feet. The zone of greatest concentration of living vegetation appeared to be in depths of six to nine feet. This included both the "submarine meadows," which reached their greatest development in the canals and cuts, and the heavy algal growth which carpeted the flats adjacent to Smack Channel. Table 1 gives a list of the algae by station and habitat data. Location of stations is given in Figures 1 and 2.

The Algal Flora and its Distribution

A total of 35 species of algae was collected of which 19 (54%) were Rhodophyta, 7 (20%) Chlorophyta, 5 (14%) Phaeophyta, and 4 (11%) Cyanophyta. The collection seems to represent groups with three phytogeographic affinities: (1) "boreal" species with apparently disjunct distributions, found along the Atlantic coast to northern or central Florida and along the northern gulf coast, but not continuous around the Florida peninsula; (2) "tropical" species found primarily in southern Florida and the West Indies, for which the Chandeleur Islands represent the northernmost extent of the known range in this area of the gulf; and (3) ubiquitous species whose phytogeographic affinities are less specific.

TABLE 1

Station distribution

Station 270. In Chandeleur Sound 1.8 miles S. E. of Martin Key. Bottom sandy, depth 10 feet, salinity 31.5 ppt, water temperature 21.0°C. Collection date: March 27, 1954.
Gracilaria foliifera (Forskal) Børgesen
Polysiphonia denudata (Dillwyn) Kützing

Station 272. In Chandeleur Sound (Smack Channel), one-half mile S. W. of Mangrove Island. Bottom muddy sand, depth 17–18 feet, salinity 30.6 ppt, water temperature 20.5°C, Secchi disk reading 8.0 feet. Collection date: March 28, 1954.
Agardhiella tenera (J. Agardh) Schmitz
Cladophora delicatula Montagne
Jania capillacea Harvey
Laurencia poitei (Lamouroux) Howe
Polysiphonia havanensis Harvey
Spyridia filamentosa (Wulfen) Harvey
Ulvella lens Crouan

Station 276. An isolated salt water pond on Chandeleur Island, east of North Island. Bottom sandy mud, depth zero to four feet, water temperature 20.5°C. Collection date: March 28, 1954.
Ectocarpus rallsiae Vickers
Enteromorpha clathrata (Roth) J. Agardh
Sphacelaria furcigera Kützing
Wrightiella tumanowiczii (Gatty) Schmitz

Station 278. Pass between North Island and Chandeleur Island. Bottom sandy mud with detritus and decomposing vegetation, depth 17–18 feet. Collection date: March 28, 1954.
Caulerpa prolifera (Forskal) Lamouroux
Eudesme zosterae (J. Agardh) Kylin
Fosliella farinosa, var. *solmsiana* (Falkenberg) Taylor
Fosliella lejolisii (Rosanoff) Howe

Station 278a. Lagoon on the lee side (west) of Chandeleur Island east of North Island. Bottom of muddy sand and covered by *Thalassia testudinum*, depth six feet. Collection date: March 28, 1954.
Achrochaetium flexuosum Vickers
Digenea simplex (Wulfen) C. Agardh
Griffithsia tenuis C. Agardh
Polysiphonia echinata Harvey

Station 282. In the Gulf of Mexico two miles north of Chandeleur Island. Depth 40–44 feet, salinity 31.6 ppt, water temperature 19.7°C. Collection date: March 29, 1954.
Enteromorpha clathrata (Roth) J. Agardh

Station 506. At the head of a cut on the lee (west) side of Chandeleur Island, two miles north of Mangrove Island. Bottom of muddy sand, depth zero to four feet. Collection date: August 25, 1954.
Laurencia poitei (Lamouroux) Howe
Lophosiphonia sacchoriza Collins and Hervey
Phaeophila dendroides (Crouan) Batters
Spirulina subsalsa Oersted, forma *oceanica* (Crouan) Gomont

Station 509. In Smack Channel one mile N. W. of Mangrove Island, Chandeleur Sound. Bottom of muddy sand, depth six feet, salinity 36.2 ppt, water temperature 29.5°C. Collection date: August 26, 1954.
Agmenellum thermale (Kützing) Drouet and Daily
Cermium byssoideum Harvey
Cladophoropsis membranacea (C. Agardh) Børgesen
Dictyota dichotoma (Hudson) Lamouroux
Gracilaria caudata J. Agardh
Hypnea musciformis (Wulfen) Lamouroux
Hypnea pannosa J. Agardh
Lyngbya gracilis (Meneghini) Rabenhorst
Lyngbya majuscula Gomont
Padina vickersiae Hoyt
Rhizoclonium kochianum Kützing
Sphacelaria furcigera Kützing

Comparing the algal flora of the Chandeleur Islands with that of the nearby and better-known Mississippi Sound, it may be seen that 21 of the 35 species (or three-fifths) of the algae from the Chandeleurs have not been recorded from Ship Island. In fact,

most of the tropical elements of the Chandeleur flora were absent from the Ship Island summer flora. Although further collecting may alter the picture somewhat, the present pattern is striking. It is tentatively suggested that the absence of many of these species from the Ship Island flora is not an accident of dispersal, but rather a failure of establishment and survival. Although habitat tolerances of most of the marine algae are poorly known, many of the species in the Chandeleur list appear to be more stenohaline than those of Ship Island. A comparative study of the two environments would undoubtedly show that the Chandeleur Island area is characterized by warmer (in winter), more saline, and less turbid waters, and that fluctuations in these environmental conditions are less pronounced there than in Mississippi Sound. Undoubtedly other more subtle environmental influences are also involved.

Annotated List of Species

Cyanophyta
Order Chroococcales
Family Chroococcaceae

Agmenellum thermale (Kützing) Drouet and Daily. References: Kützing, 1843 (as *Merismopedia thermalis*); Tilden, 1910 (as *M. convolutum* Brebisson); and Drouet and Dailey, 1956. At a depth of six feet in Smack Channel one mile N.W. of Mangrove Island (Station 509) growing around the base of *Hypnea musciformis.*

Order Oscillatoriales
Family Oscillatoriaceae

Spirulina subsalsa Oersted, forma *oceanica* (Crouan) Gomont. References: Oersted, 1842; Gomont, 1892; Tilden, 1910; and Humm and Caylor, 1957. At the western side of the main island in shallow water (Station 506) on *Laurencia poitei.*

Lyngbya gracilis (Meneghini) Rabenhorst. References: Meneghini, 1844 (as *Leibleinia gracilis*); Rabenhorst, 1865; Gomont, 1892; and Tilden, 1910. In six feet of water on *Hypnea pannosa,* western side of the main island at Station 509.

Lyngbya majuscula Gomont. References: Gomont, 1892; and Tilden, 1910. Entangled in *Cladophoropsis membranacea* at Station 509.

Chlorophyta
Order Ulotrichales
Family Chaetophoraceae

Phaeophila dendroides (Crouan) Batters. References: Crouan and Crouan, 1867 (as *Ochlochaete dendroides*); Batters, 1902; Taylor, 1928 (as *P. floridearum* Hauck); and Newton, 1931. At the western side of the main island (Station 506) on *Laurencia poitei* in shallow water.

Ulvella lens Crouan. References: Crouan and Crouan, 1859; Børgesen, 1914; and Humm and Caylor, 1957. In Smack Channel at the western side of the main island (Station 272) on *Laurencia poitei* in about 18 feet of water.

Order Ulvales
Family Ulvaceae

Enteromorpha clathrata (Roth) J. Agardh. References: Roth, 1806 (as *Conferva clathrata*); J. G. Agardh, 1882–83; Kylin, 1949; and Taylor, 1957. In a salt water pond on the main island (Station 276) and adrift in 44 feet of water at the north end of the main island. This species may be present only in the winter and spring. It was one of the slender forms referred in the past to *E. crinita* (Roth) J. Agardh but which Taylor (1957) regards as conspecific with *E. clathrata*. There are certainly other species of *Enteromorpha* among the islands.

Order Cladophorales
Family Cladophoraceae

Cladophora delicatula Montagne. References: Montagne, 1850; Collins, 1909; and Taylor, 1928. Smack Channel between North Island and the main island on *Laurencia poitei* in about 18 feet of water (Station 272).

Cladophoropsis membranacea (C. Agardh) Børgesen. References: C. Agardh, 1824; Harvey, 1858; Børgesen, 1905; and Collins, 1909. At the western side of the main island (Station 509) in six to nine feet of water, a loose clump.

Rizoclonium kochianum Kützing. References: Kützing, 1845; Collins. 1909; and Newton, 1931. At the western side of the main island in six to nine feet of water, unattached (Station 509). On the basis of descriptions given by Vickers and Shaw (1908) and Collins (1909) this material agrees better with *R. kerneri* Stockmayer with respect to cell length as the cells were mostly 2 to 3½ times as long as wide. Newton (1931) includes material with cells 3½ to 4½ times as long as broad in *R. kochianum*. A critical study of the two species might show them to be better regarded as varieties of the same species.

Order Siphonales
Family Caulerpaceae

Caulerpa prolifera (Forsskal) Lamouroux. References: Forsskal, 1775; Lamouroux, (1809); and Collins, 1909. In about 18 feet of water in the pass between North Island and the main Chandeleur Island (Station 278). This species is evidently the northernmost one of the genus in the North Atlantic. In North Carolina it is found only some distance off shore in several fathoms. In Alligator Harbor, south of Tallahassee, Florida, in the Gulf of Mexico it is found just below low tide.

Phaeophyta
Order Ectocarpales
Family Ectocarpaceae

Ectocarpus rallsiae Vickers. References: Vickers and Shaw, 1908; and Børgesen, 1914. In an isolated salt water pond on the main Chandeleur Island (Station 276). It is surprising that this should be the only species of *Ectocarpus* in the collections for surely there are others that are at times more common and conspicuous.

Order Sphacelariales
Family Sphacelariaceae

Sphacelaria furcigera Kützing. References: Kützing, 1855; Collins and Hervey, 1917; and Blomquist and Humm, 1946. In an isolated salt water pond on the main Chandeleur Island (Station 276) on *Spyridia filamentosa* and in Smack Channel about one mile N.W. of Mangrove Island (Station 509) in six to nine feet of water on *Padina vickersiae*.

Order Chordariales
Family Chordariaceae

Eudesme zosterae (J. Agardh) Kylin. References: J. Agardh, 1841 (as *Myriocladia zosterae*); Kylin, 1933; Taylor, 1937 (as *Aegira zosterae*); and Taylor, 1957. From the channel between North Island and the main island on a drifting leaf of *Thalassia testudinum* which probably grew on the nearby flats. This is a winter and spring species in the Gulf of Mexico where its characteristic habitat is leaves of *Thalassia*. It appears annually in November or December, reaches a peak of abundance in March, and usually disappears in late April or May.

Order Dictyotales
Family Dictyotaceae

Dictyota dichotoma (Hudson) Lamouroux. References: Hudson, 1798 (as *Ulva dichotoma*); Lamouroux, 1809; and Børgesen, 1914. In Smack Channel about one mile N.W. of Mangrove Island in about six feet of water (Station 509). Along the Atlantic coast this is the northernmost species of the genus. Its northern known limit is Beaufort, North Carolina, where it is abundant each year from April to November. It is probably absent also in the northern Gulf of Mexico during the winter months. *D. cervicornis* has been reported (Humm and Caylor, 1957) in Mississippi Sound.

Padina vickersiae Hoyt. References: Hoyt, 1917–18; and Taylor, 1928. In Smack Channel about one mile N.W. of Mangrove Island in about six feet of water (Station 509). This species also reaches its northern limit near Beaufort, North Carolina, along the Atlantic coast of North America and it is the northernmost species of the genus. Like *Dictyota*, it is absent during the winter months in the northern part of its range. Information on its seasonal behavior in the northern Gulf of Mexico is not yet available, but there are indications that it persists the year around.

Rhodophyta
Order Nemalionales
Family Chantransiaceae

Achrochaetium flexuosum Vickers. References: Vickers, 1905; and Taylor, 1957. On *Digenea simplex* from a bed of *Thalassia* on the lee side (west side) of Chandeleur Island (Station 278a).

Order Cryptonemiales
Family Corallinaceae

Fosliella farinosa (Lamouroux) Howe, var. *solmsiana* (Falkenberg) Taylor. References: Lamouroux, 1816 (as *Melobesia farinosa*); Howe, 1920; and Taylor, 1928 (as *Melobesia*). In Smack Channel between North Island and the main Chandeleur Island on a drifting leaf of *Thalassia*.

Fosliella lejolisii (Rosanoff) Howe. References: Rosanoff, 1866 (as *Melobesia lejolisii*); Howe, 1920; and Taylor, 1928 (as *Melobesia*). On *Caulerpa prolifera* in the pass between North Island and Chandeleur Island in about 18 feet of water (Station 278) and on a drifting leaf of *Thalassia* in Smack Channel about one-half mile S.W. of Mangrove Island (Station 272) and on a sponge from 15–18 feet of water in the pass between North Island and Chandeleur Island (Station 278).

Order Gigartinales
Family Solieriaceae

Agardhiella tenera (J. Agardh) Schmitz. References: J. Agardh, 1841 (as *Gigartina tenera*); Harvey, 1853 (as *Solieria chordalis*); Schmitz, 1889; and Hoyt, 1917–1918. In Smack Channel at a depth of 18 feet about one-half mile S.W. of Mangrove Island (Station 272). Along the Atlantic Coast of the United States this species is most abundant during the spring and summer north of the Virginia Capes and in winter and spring to the south. In its southern range there are some plants that exhibit different seasons of growth.

Family Hypneaceae

Hypnea pannosa J. Agardh? References: J. Agardh, 1851; and Taylor, 1928. On a muddy sand bottom in Smack Channel about one mile N.W. of Mangrove Island (Station 509). This is a relatively soft, delicate, and rather entangled species of *Hypnea*. Internally the Chandeleur plant shows a distinct difference in diameter of the pericentral cells in contrast to the much smaller cortical cells, which are also of fewer layers than in most of the other species. Identification of species of the genus *Hypnea*, other than typical *H. musciformis*, will continue to be difficult and largely tentative until a monographic study of the genus is made. Collins and Hervey (1917, p. 113) comment on this problem.

Hypnea musciformis (Wulfen) Lamouroux. References: Wulfen *in* Jacquin, 1789 (as *Fucus musciformis*); Lamouroux, 1813; and Collins and Hervey, 1917. Smack Channel about one mile N.W. of Mangrove Island (Station 509) in about six feet of water. This species is probably very abundant among the Chandeleur Islands during the summer and fall.

Family Gracilariaceae

Gracilaria caudata J. Agardh. References: J. Agardh, 1851; and Børgesen, 1920. Smack Channel about one mile N.W. of Mangrove Island (Station 509) in six to nine feet of water. This species has been reported at the Virgin Islands by Børgesen, who also indicates that it is known from Mexico, presumably the Gulf of Mexico. It has been reported in abundance in Tampa Bay, Florida (Humm, 1944).

Gracilaria foliifera (Forsskal) Børgesen. References: Forsskal, 1775; Hoyt, 1917–18 (as *G. multipartita* (Clemente) J. Agardh); Taylor, 1928 (as *G. lacinulata* (Vahl) Howe); and Taylor, 1957. In about 10 feet of water, Chandeleur Sound, 1.8 miles S.E. of Martin Key (Station 270). This is the most common species of *Gracilaria* in the northern Gulf of Mexico where it is present the year around. Although the synonyms given in the list of references above have been widely accepted, there is evidence from other areas that there are two species involved here. However, *G. foliifera* seems to be the correct name for the material referred to here.

Order Ceramiales
Family Ceramiaceae

Ceramium byssoideum Harvey. References: Harvey, 1853; Collins and Hervey, 1917 (as *C. transversale*); Taylor, 1928; and Mazoyer, 1938 (as *C. gracillimum* (Griffiths) Harvey, var. *byssoideum* (Harvey) Mazoyer). Smack Channel about one mile N.W. of Mangrove Island (Station 509) in six feet of water on *Hypnea musciformis.* Dr. Genevieve Feldman-Mazoyer regards *C. byssoideum* as a variety of *C. gracillimum* as a result of her studies of Mediterranean material. Since *C. gracillimum* has not yet been reported along the Atlantic coast of North America and we have not studied typical material of it, we follow Howe's (1920) use of the name *C. byssoideum.*

Griffithsia tenuis C. Agardh. References: C. Agardh, 1828; Collins and Hervey, 1917; and Howe, 1920. On *Digenea simplex* from a lagoon on the west side of Chandeleur Island at a depth of six feet near Station 278. Tetrasporangia on this plant were up to 75 microns in diameter.

Spyridia filamentosa (Wulfen) Harvey. References: Wulfen, 1803 (as *Fucus filamentosus*); Harvey *in* Hooker, 1833; and Hoyt, 1917–18. In Smack Channel, Chandeleur Sound, one-half mile S.W. of Mangrove Island (Station 272) in about 18 feet of water, apparently loose.

Family Rhodomelaceae

Digenea simplex (Wulfen) C. Agardh. References: Wulfen, 1803 (as *Conferva simplex*); C. Agardh, 1822; and Taylor, 1928. From a lagoon with an abundance of *Thalassia testudinum* on the west side of Chandeleur Island at a depth of six feet near Station 278. This is a typical habitat although it is usually in shallower water.

Laurencia poitei (Lamouroux) Howe. References: Lamouroux, 1805 (as *Fucus poitei*); Howe, 1905; and Taylor, 1928. In Smack Channel, Chandeleur Sound, one-half mile S.W. of Mangrove Island in 18 feet of water (Station 272); at the head of a cut on the west side of Chandeleur Island two miles north of Mangrove Island (Station 506). This species is often found in *Thalassia* beds with *Digenea.*

Lophosiphonia sacchoriza Collins and Hervey?. References: Collins and Hervey, 1917; and Humm and Caylor, 1957. At Station 506 (described above) creeping upon *Laurencia poitei.* This species was discussed and figured by Humm and Caylor, who found it in Mississippi Sound, indicating that it may be more appropriately placed in the genus *Polysiphonia.*

Polysiphonia echinata Harvey. References: Harvey, 1853; and Taylor, 1928. On *Digenea simplex* from Station 278.

Polysiphonia havanensis Montagne. References: Montagne, 1837; Howe, 1920; and Taylor, 1928. In Smack Channel, Chandeleur Sound, one-half mile S.W. of Mangrove Island (Station 272) in 18 feet of water.

Polysiphonia denudata (Dillwyn) Kützing. References. Dillwyn, 1809 (as *Conferva denudata*); Kützing, 1858; and Hoyt, 1917–18. On *Thalassia* at a depth of 10 feet, Chandeleur Sound, 1.8 miles S.E. of Martin Key (Station 270).

Wrightiella tumanowiczii (Gatty) Schmitz. References: Gatty *in* Harvey, 1853 (as *Dasya tumanowiczii*); Schmitz, 1893; Collins and Hervey, 1917; and Taylor, 1928. In an isolated salt water pond on Chandeleur Island (Station 276). This species has

not been reported previously from the northern Gulf of Mexico, and its presence in an isolated pond seems remarkable. Its occurrence in the area may be sporadic and temporary.

Summary

Thirty-five species of marine algae were collected among the Chandeleur Islands, northern Gulf of Mexico. Ecological and phytogeographic relations of these algae are discussed and an annotated list of species is included.

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The Phytoplankton of Apalachee Bay and the Northeastern Gulf of Mexico[1]

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Abstract

Routine phytoplankton collections were made during the years 1953 to 1955 in Apalachee Bay, in the northeastern Gulf of Mexico, and along the west coast of Florida. A total of 116 diatom species, 17 dinoflagellate species, one coccolithophore, two silicoflagellates, and one blue-green species were identified.

The diatoms were most numerous in individuals and species. *Rhizosolenia alata* Brightwell was the most abundant summer species and *Chaetoceros decipiens* Cleve was the most abundant winter species. The ranges of 23 species are extended to the gulf.

Ceratium furca (Ehrenberg) Clap. and Lach. was the most common and abundant dinoflagellate. *Podolampas elegans* Schütt was surprisingly abundant.

Trichodesmium thiebauti Gomont was present on only one occasion in November, 1953.

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Editor's Note: Figures and Keys were added at the request of the editors to aid instruction and research on Gulf phytoplankton.

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Introduction

Studies on the phytoplankton of the Gulf of Mexico have been rather limited. Davis (1954) reviews most of these efforts. The recent occurrence of "red tides" along the west coast of Florida has had a stimulating effect and a few specialized papers have appeared recently (Lasker and Smith, 1954; Gunter *et al.*, 1948).

Davis (1950) published a summary of his investigations which were based mainly on single samples from several localities along the gulf coast of Florida. King (1950) made collections in the same area, excepting the "panhandle," but his data are mostly qualitative and identifications usually were made to genus only. Freese (1952) made extensive collections of diatoms at Rockport, Texas, and this work constitutes the most recent investigation in the gulf to date. Conger (1954) reports that he is studying collections of diatoms made on the west coast of Florida but has not published on them thus far.

The present account considers the occurrence of planktonic diatoms, dinoflagellates, coccolithophores, silicoflagellates, and blue-green algae from the vicinity of Alligator Harbor, Franklin County, Florida. Collections were made at bi-weekly intervals during 1953–1955 from within Alligator Harbor itself, to a distance thirty miles from shore. In addition, a number of samples were taken at points along the west coast of Florida.

METHODS

In most cases one liter of water was preserved with neutralized formalin and concentrated in a Foerst plankton centrifuge. Examinations and routine counts were made under a magnification of 400 X with phase contrast optics. A Sedgwick Rafter counting cell contained the sample and examinations were made in water. Aliquots of all the samples were also made into permanent mounts, using Hyrax and Pleurax mountants, and these were used under oil immersion for more detailed study.

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Mr. Paul S. Conger varified several identifications made by the author. Assistance from the National Science Foundation and the Jessup Fund of the Philadelphia Academy of Sciences is gratefully acknowledged.

Diatoms

There are about 18 papers on the diatoms and diatom ecology of the Gulf of Mexico, over half of them being published in the latter part of the 19th century. There are, apparently, a number of unpublished lists and compilations. Conger (1954), for example, mentions an unpublished list of 60 genera and 500 species of diatoms from the gulf.

Mobile Bay (Cunningham, 1889; Cox, 1901), the west coast of Florida (Davis, 1950; King, 1950) and Rockport, Texas (Freese, 1952) are the most studied areas of the gulf.

The classification scheme, based on the morphology of the diatom frustule, of Schütt (1896) and modified by Hustedt (1930) is the most widely used. Hendey (1937) has proposed a slight modification of Schütt's original classification, dropping the artificial division into two suborders, the Centricae and the Pennatae. Instead, in the class Bacillariophyceae he erects one order, the Bacillariales, which is divided into ten suborders. The rest of the classification is not significantly altered. This writer feels that Hendey's scheme best expresses the true phylogenetic positions of the various taxa as we know them today and has chosen to use his classification here.

Where available, supplementary information concerning range, normal environment, *etc.* are given to help in understanding Florida and gulf distributions. However, ecological considerations *per se* are not included and will be treated elsewhere. In matters of nomenclature Hustedt (1930) has been followed for the most part. Since diatom distribution is so poorly known for the Gulf of Mexico, comparisons are made with occurrences at Beaufort, North Carolina (Manly, 1953) and Rockport, Texas (Freese, 1952). Beaufort and Apalachee Bay have somewhat similar hydrographic climates (Curl, 1956).

This study revealed a total of 116 species grouped into 51 genera. There were 30 genera for which were found only one species each. Of the remaining 21 genera, four contained the largest number of species. *Coscinodiscus* had 9; *Biddulphia*, 9; *Rhizosolenia*, 12; and *Chaetoceros*, 18. The latter two genera included between 8 and 65 per cent of the individuals found at any given time in 1954. In 58 per cent of the samples these two genera included 50 per cent or more of the individuals present. It follows that these genera were responsible for most of the phytoplankton biomass during the year.

The geographic distribution of diatoms, particularly marine pelagic species, is fairly well known. A large number of diatom species are considered to be "cosmopolitan." The prevalence of this kind of distribution implies genetic stability over a long period, broad physiological tolerances, and a means of transportation. All three factors are actually operating (Patrick, 1948 and 1954; Sverdrup *et al.*, 1942, Chap. XV). Patrick (1948) refutes the proposition that diatoms are generally cosmopolitan, stating that endemism may range from 10 to 30 per cent in a local flora. However, such a small percentage implies that the other three-fourths of the species are either cosmopolitan or have broad ranges. It would appear, *prima facia*, that the distribution of pelagic diatoms, with other organisms, will be governed by their physiological requirements and the state of their environment. These requirements are unknown for all practical purposes.

Cleve (1899) devised a classification of plankton types based on the currents in which the plankton were found and assumed an essential stability of composition. Hjort and Gran (1899) expressed the idea that the plankton composition in an ocean current would depend upon the time of year and stressed the importance of ecological conditions as opposed to common origin. Gran (1902) proposed a zonal classification embodying arctic, boreal, and temperate zones. The terms arctic, boreal, etc. are unfortunate since they denote geographic areas. Such a usage is untenable, for many species designated as "arctic" occur in the subtropics, *e.g.*, *Chaetoceros decipiens* Cleve and *Nitzschia seriata* Cleve. Such is the case in the Gulf of Mexico. A number of "arctic" diatoms occur here when the water temperature is sufficiently low, *i.e.*, in the vicinity of 15°C. Likewise a number of "tropical" species occur in the region, either brought in by currents or capable of overwintering.

A total of 23 species are reported from the Gulf of Mexico for the first time. These are:

Melosira dubia Kützing
M. nummuloides (Lyngbye) Agardh
Coscinodiscus excentricus Ehrenberg
C. kutzingii A. Schmidt
Biddulphia aurita (Lyngbye) Brébisson *et* Godey
B. obtusa (Kützing) Ralfs
B. sinensis Greville
Triceratium reticulum (Ehrenberg) Boyer
Chaetoceros dichaetum Ehrenberg
C. glandazi Mangin
C. diversum Cleve
C. debile Cleve
C. gracile Schütt
Rhizosolenia bergonii Peragallo
R. castracane Peragallo
R. cylindrus Cleve
Leptocylindrus danicus Cleve
Striatella interrupta (Ehrenberg) Heiberg
Achnanthes manifera Brun
C. scutellum Ehrenberg

and three species hitherto known only from the type locality:

Amphora micans Schmidt. Campeche Bay
Cocconeis disculoides Hustedt. Beaufort, N. C.
Camplyodiscus punctulatus (Grun) Schmidt. Campeche Bay

The diatoms characteristic to Campeche Bay, as well as those endemic there, are especially interesting. The similarity of flora between this region and the Philippine Islands has been discussed by Mann (1925). Since two diatoms, until now found only in Campeche Bay/Philippine Islands, were also found in the northern Gulf of Mexico, it is not unreasonable to suspect that the ranges of others might also extend throughout the gulf. It will be noted that the majority of species listed by Mann with this distribution belongs to the genus *Navicula*. This genus was ignored taxonomically in the present study because of the small biomass represented.

An investigation of endemism in neritic and littoral Gulf of Mexico diatom species would be very welcome.

A majority of the common species and a few of the rare ones were identified in wet mounts during routine counts. Identified specimens on permanent slides are not available for all species found in these collections. However, the author has a collection of permanent slides made from most of the collections, which include some identified specimens, identified herein as M 100 to M 105, and C 200, C 205, and C 206. The Oceanographic Institute at Florida State University is the repository of a set of identified specimen slides, identified as slides C 201 to C 204. The number of the slide on which the specimen occurs will be found in parentheses following the species name.

The designations "warm water" and "cold water" have been used in preference to "arctic" and "tropical," since many species considered to be "arctic" occur in the Gulf of Mexico when the water temperature is sufficiently low.

List of Genera:

I. *Melosira*. p. 285
II. *Skeletonema*. p. 285
III. *Stephanopyxis*. p. 286
IV. *Thalassiosira*. p. 286
V. *Schroederella*. p. 286
VI. *Coscinodiscus*. p. 286
VII. *Actinocyclus*. p. 287
VIII. *Hemidiscus*. p. 287
IX. *Actinoptychus*. p. 287
X. *Eupodiscus*. p. 288
XI. *Auliscus*. p. 288
XII. *Pseudauliscus*. p. 288
XIII. *Biddulphia*. p. 289
XIV. *Bellarochia*. p. 290
XV. *Cerataulina*. p. 290
XVI. *Triceratium*. p. 290
XVII. *Lithodesmium*. p. 291
XVIII. *Hemiaulus*. p. 291
XIX. *Eucampia*. p. 291
XX. *Climacodium*. p. 291
XXI. *Streptotheca*. p. 292
XXII. *Terpsinöe*. p. 292
XXIII. *Chaetoceros*. p. 292
XXIV. *Bacteriastrum*. p. 296
XXV. *Rhizosolenia*. p. 296
XXVI. *Guinardia*. p. 298
XXVII. *Leptocylindrus*. p. 299
XXVIII. *Corethron*. p. 299
XXIX. *Asterionella*. p. 299
XXX. *Synedra*. p. 299
XXXI. *Thalassiothrix*. p. 299
XXXII. *Thalassionema*. p. 300
XXXIII. *Campylosira*. p. 300
XXXIV. *Dimerogramma*. p. 300
XXXV. *Plagiogramma*. p. 300
XXXVI. *Licmophora*. p. 300
XXXVII. *Rhabdonema*. p. 300
XXXVIII. *Grammatophora*. p. 300
XXXIX. *Striatella*. p. 300
XL. *Achnanthes*. p. 301
XLI. *Cocconeis*. p. 301.
XLII. *Navicula*. p. 301
XLIII. *Pleurosigma*. p. 301
XLIV. *Gyrosigma*. p. 301
XLV. *Trachyneis*. p. 302
XLVI. *Tropidoneis*. p. 302
XLVII. *Amphora*. p. 302
XLVIII. *Nitzschia*. p. 302
XLIX. *Surirella*. p. 303
L. *Campylodiscus*. p. 303

The following analytical keys to the diatom genera are artificial in that the characters used are those most easily determined in fresh material rather than those commonly accepted as diagnostic of particular phyletic groupings. Keys to the diatoms commonly fail at the point where it must be determined that the specimen in question possesses a raphe or central canal. Hendey (1937) avoids this difficulty by presenting eight initial choices after which his key is dichotomous. To avoid ambiguity the entry into the present key uses the old discrimination between the centric and pennate forms.

It must always be borne in mind that a key will take one to the included forms only. If not excluded at an early stage the choice will come down to the name listed and

any number of unlisted names. Therefore, unless exhaustive (which this key is not), the identification must be tentative until similar genera and/or species are positively excluded. For generic determination the most complete and concise treatment appears in Engler and Prantl's *Die Naturlichen Pflanzenfamilien* (1928, 2nd ed.) in which the diatoms are summarized by G. Karsten.

For the most part, the figures are from actual specimens and are all drawn to the same scale. Complicated structures such as diatoms can be portrayed in a variety of ways. Recourse has been made to drawings in all the available taxonomic texts for the best way of portraying different structures and no claim is made for originality of treatment.

Key to Genera of Diatoms

1a	Cell drum-like or cylindrical and longer than wide. Valve with radiating or concentric markings arranged around excentric or central points. Spines frequently present.	2
1b	Cell elongated in valve view. Valves bilaterally symmetrical with markings arranged around a central line. Spines, if present, very short.	3
2a	Cell drum-like. Valve sculpturing radially symmetrical. Numerous fine spines usually present on valve margin.	4
2b	Cells cylindrical with many intercalary bands. Center of valve symmetry displaced toward margin. Cells may be joined at valve face.	5
2c	Cells drum-like. Valve circular, elliptical or three-cornered. Valves with one or more processes at corners forming short horns or long spines.	6
3a	Cells usually elongate or wedge-shaped. Cell ends unlike.	17
3b	Cells box-like, usually seen in girdle view. Both cell ends similar.	29
4a	Radial markings uninterrupted. No eyes present but with short or long spines.	7
4b	Radial markings uninterrupted. With four pores placed at valve margin. Without spines.	*Eupodiscus*
4c	Radial markings interrupted by ribs, undulations or transparent areas. One or more eyes frequently present. Without spines.	8
5a	Excentric process present.	16
5b	Excentric process absent. Cells longer than broad, attached to form chains by flat valve.	*Leptocylindrus*
6a	Valves with two setae, much longer than cells. Frequently forming loose chains.	12
6b	Valves with two or more short processes.	13
7a	Cells usually united by spines, threads or toothed valve margins into chains. Sometimes in gelatinous colonies.	9
7b	Cells solitary, marginal spines always short.	*Coscinodiscus*
8a	Valves with no eyes at margin.	*Actinoptychus*
8b	Valve with one eye at margin.	10
8c	Valve with two eyes at margin.	11
9a	Cells united by a circlet of spines only. May be solitary.	14
9b	Cells united face to face or by a central thread.	15
10a	Valve circular.	*Actinocyclus*
10b	Valve semilunar, cells sometimes joined to form a sphere.	*Hemidiscus*

11a A central clear area present. *Auliscus*
11b A central clear area absent. *Pseudauliscus*
12a Setae forking. *Bacteriastrum*
12b Setae not forking. *Chaetoceros*
13a Valves with two corners. 18
13b Valves with three or more corners. 19
14a Valve with fine or indiscernible markings. Cell with long spines, free or in chains. 20
14b Valve coarsely marked. Cells united by stout spines. *Stephanopyxis*
15a Cells united at valve face by toothed margins. No spines. *Melosira*
15b Cells joined by a central thread. Fine marginal spines. Sometimes in a gelatinous matrix. *Thalassiosira*
16a Intercalary bands circular, collar-shaped near girdle. Valve flat with a small tooth at margin. *Guinardia*
16b Intercalary bands rhombic or scale like. Process a blunt horn or sharp spine. *Rhizosolenia*
17a Cell wedge-shaped in girdle and valve view *Licmophora*
17b Cell attenuated, one end pointed, the other obtuse or flattened in valve view. 28
18a Strongly siliceous cell with two horns on valve margin and frequently two spines on valve face. *Biddulphia*
18b Without spines on valve. Weakly siliceous. The process either very short and blunt or long and tapering. 22
19a Thin, hollow spine in center of valve. Valve with marginal membrane by which cells are connected. *Lithodesmium*
19b Cells strongly siliceous, marked. No central spine. Each corner of valve produced into a short horn by which cells may be joined. *Triceratium*
20a Cells free, with long, fine spines, directed outwards. Valves hemispherical. *Corethron*
20b Cells attached by marginal spines. 21
21a Cells without intercalary bands, spherical to cylindrical. Valve markings very fine. *Skeletonema*
21b Cells, with many intercalary bands, joined by very short spines. *Schroderella*
22a Processes short and blunt. 23
22b Processes long and tapering. *Hemiaulus*
23a Valves joined by processes and valve faces. 24
23b Valves joined by processes only, no spines on processes. 25
24a No aperature visible between valves. 26
24b Small aperature adjacent to processes. 27
25a Cells with two blunt processes by which cells are joined to form spiral chains. Valve noticeably marked. Intercalary bands present. *Eucampia*
25b Cells joined by short tapering processes. Cell weakly siliceous, no visible markings. Intercalary bands absent. *Climacodium*
26a Cells flattened and twisted through 90° on the long axis. United by short, blunt processes to form ribbons. *Streptotheca*
26b Cells quadrangular in girdle view, elliptical or undulating in valve view. Cells without processes, free or joined at corners to form short chains. *Terpsinöe*

27a Cells cylindrical, with two very short, blunt processes ending in fine spines, by which the cells are joined to form twisted chains. Cells longer than broad. *Cerataulina*

27b Cells flattened, with two very short, blunt processes, lacking spines. Joined to form ribbon-like chains. Cell broader than long. *Bellarochea*

28a Cells linear with base enlarged. Joined at base to form star-like colonies. *Asterionella*

28b Cells linear and elongated. Base slightly swollen and pointed. Head obtuse. Cells free or joined at base. *Thalassiothrix*

29a Cells rectangular. Intercalary bands present. Septae placed in the bands. 30

29b Intercalary bands absent. No septae. 31

30a Numerous intercalary bands with short septae in alternate bands. Valves with delicate punctate striae. *Striallela*

30b Numerous intercalary bands, strongly punctate, with numerous septae. *Rhabdonema*

30c Few intercalary bands. Septae large, undulating, extending toward center of cell. *Grammatophora*

31a Raphe absent in one or both valves. 32

31b Raphe present in both valves, frequently strongly developed to form a keel. Cell may be bent in several planes. 33

32a Raphe in one valve only. 34

32b Raphe absent in both valves. 35

33a Cell without keel, wings or membranes. Marked with striae and punctae but not ribs or costae. 36

33b Cell with obvious keels, wings or membranes. Marked with punctae, costae or both. 37

34a Markings similar on both valves. *Achnanthes*

34b Markings unlike on both valves. *Cocconeis*

35a Cell inflated at center valve view, constricted near the ends. 38

35b Cell not inflated in center. 39

36a Cell in valve view not straight but either bent or lop-sided with reference to midline. 40

36b Cell linear and symmetrical with reference to midline. 41

37a Cell with a keel in the midline. Cell very inflated. *Tropidoneis*

37b Cell with an excentric keel in valve margin, extending part or all of the way around the valve. 42

38a Valves with one or more transapical ribs penetrating more or less deeply to form a false septum. Cells joined at ends and center of valves to form chains. *Plagiogramma*

38b Valves with ribs produced to form numerous short spines. Cells bent at center and joined at center to form chains. *Campylosira*

39a Cells oblong, frequently joined at corners to form zig-zag or star-like colonies. Valve with tiny spines at regular intervals on margin and at ends. *Thalassionema*

39b Cells oblong, free and without spines. *Synedra*

40a Cell linear but lop-sided. Markings at right angles to midline. Intercalary bands present. *Amphora*

40b Valves sigmoid. Intercalary bands absent. 43

41a Valve laminate, composed of three closely superimposed layers with differing structures. *Trachyneis*
41b Valve simple. *Navicula*
42a Cell with a distinct, excentric, punctuate keel in each valve. Without ribs or costae. *Nitzschia*
42b Cell with keel in valve margin and running around entire valve. Costae and ribs prominent. 44
43a Markings rectilinear and oriented parallel to midlines. *Pleurosigma*
43b Ornamentation oblique with reference to midline. *Gyrosigma*
44a Valve oblong sometimes twisted about long axis. *Surirella*
44b Valves sub-circular, saddle-shaped, united at right angles to one another. *Campylodiscus*

Suborder DISCINEAE

Family COSCINODISCACEAE

Subfamily MELOSIROIDEAE

Genus I. *Melosira* Agardh

M. dubia Kützing. Bacill., p. 53, Plate 3, Figure 8, 1844. (Figure 2). Neritic and littoral. Euryhaline. North Sea, coasts of England and India. A few cells were observed in Apalachee Bay in February, 1955. Rare. Not reported elsewhere in the Gulf of Mexico.

M. nummuloides (Lyngbye) Agardh, Syst. Alg., p. 8, 1824. (Figure 3). Neritic. Euryhaline. Temperate species. Atlantic coasts of the United States and Europe. While this species was reported as abundant throughout the year at Beaufort, N.C., it is not reported from Rockport, Tex. or from the west coast of Florida and only a few cells were occasionally noted in Apalachee Bay.

M. sulcata (Ehrenberg) Kützing, Bacill., p. 55, Plate 2, Figure 7, 1844. (M 100, C 204). (Figure 1). Littoral, neritic, and pelagic. Cosmopolitan. Temperate species. This is a very abundant species along the Florida west coast. It is more abundant in the protected waters of Alligator Harbor than in Apalachee Bay. In the latter locality it averaged 17,450 cells/l in October, 1954 and is common there from March to October. The frustules are very abundant in the bottom deposits from the vicinity of Cape San Blas. It is reported rare at Rockport, Tex.

Subfamily SKELETONEMOIDEAE

Genus II. *Skeletomena* Greville

S. costatum (Greville) Clevel, Bih. svensk Vetensk Akad. Handl. 5:18, 1878. (Figure 4). Neritic. Euryhaline and eurythermal. Cosmopolitan. Reported from all seas except Antarctic. This is one of the most common diatoms in the gulf, particularly in the winter months. It is abundant at Rockport, Tex., in February, but was considered a "dominant" at Fort Meyers, Fla., in July, 1947. Davis (1950) attested to its eurythermal nature. In Apalachee Bay it is abundant from February through April (up to 64,000 cells/l in March, 1954), reoccurring again in August and September. *Skeletonema* was quite abundant at Panama City, Fla. in December, 1954, averaging 95,000 cells/1.

Genus III. *Stephanopyxis* Ehrenberg

S. palmeriana (Greville) Grunow, Denkschr. Akad. Wiss. Wien, 48:90, 1884. (C 200). (Figure 5). Oceanic. Warm water, high salinity species. Atlantic Ocean, Mediterranean, and Indian Ocean. While considered common to abundant at both Rockport, Tex. and Beaufort, N.C., this species is present in Apalachee Bay in March and February only and then not in large numbers. It was most common offshore. On the west coast of Florida it was most common a hundred miles offshore.

Subfamily THALASSIOSIROIDEAE

Genus IV. *Thalassiosira* Cleve

T. decipiens (Grunow) Jørgensen. Bergens Mus. Skr., 7:96, Plate 6, Figure 3, 1905. (Figure 6). Neritic. Cool temperate species. North Atlantic Ocean, Pacific coast of United States, Peru, Chile, and Mediterranean Sea. Listed as abundant in winter at Beaufort, N.C., common at Rockport, Tex. Only sparingly present in Apalachee Bay in January.

Genus V. *Schroederella* Pavillard

S. delicatula (Peragallo) Pavillard, Bull. Soc. bot. Fr., 58:126, 1913. (Figure 7). Neritic. "Favors warm water of fairly low salinity" (Hendey, 1937). Both sides of Atlantic Ocean, west coast of Africa, Mediterranean, California coast, and Java Sea. Present in Apalachee Bay in inshore waters in the spring.

Subfamily COSCINODISCOIDEAE

Genus VI. *Coscinodiscus* Ehrenberg

C. centralis Ehrenberg. Phys. Akad. Wiss. Berl., p. 129, 1840. (C 204). (Figure 8). Oceanic. Temperate species. Cosmopolitan. Very rare in Apalachee Bay. Not reported from elsewhere in the gulf or at Beaufort, N.C.

C. concinnus Smith. Syn. Brit. Diat., 2:85, 1853–56. (Figure 9). Neritic. Common in temperate and subtropical seas in water of high salinity. Not common in Apalachee Bay; found 30 miles from shore.

C. denarius A. Schmidt. Atlas, Plate 57, 1878. (C 205). (Figure 10). Neritic. Warm water species. Barbados, Campeche Bay, and California coast. Not heretofor reported from the northern Gulf of Mexico. It is present in small numbers from November to May in Apalachee Bay in the plankton and frustules can be found at other times in the sediments.

C. excentricus Ehrenberg. Phys. Akad. Wiss. Berl., p. 146, 1840. (M 104, C 204) (Figure 11). Oceanic. World-wide. Present throughout the year in Apalachee Bay, but never abundant. It is possible that centrifuging destroys the delicate frustules of this species as well as those of *C. concinnus*, and both species could become abundant without being especially noticed when this method of concentrating is used. Net tows, however, never revealed large numbers of *C. excentricus*.

C. granii Gough. North Sea Fish. Invest., No. 2:338, Figure 313, 1905. (C 203). (Figure 12). Neritic. Eurythermal. Widespread. Common at Rockport, Tex.; not reported at Beaufort, N.C. Found in March, 1954 offshore and in March, 1955 in Alligator Harbor. Only a few cells were noted.

C. kutzingii A. Schmidt. Atlas, Plate 57, Figures 17, 18, 1876. (C 205). (Figure 13). Cold water. North Sea and California. This very distinctive species was found in several samples in September, 1954. Apparently the diatom is able to survive the high water temperatures of summer (ca. 30° C). To the author's knowledge this diatom has not been reported from the Atlantic coast south of the Gulf of Maine. Boyer (1927) lists the species but does not give a locality.

C. oculus iridis Ehrenberg. Phys. Abh. Akad. Wiss., Berl., p. 147, 1841b. (C 200). (Figure 14). Oceanic. Cosmopolitan. Not previously reported from the gulf. In Apalachee Bay a few cells were found in March, 1955. Recorded as not common at Beaufort, N.C.

C. radiatus Ehrenberg. Phys. Abh. Akad. Wiss. Berl., p. 148, Plate 3, Figure 1, 1840. (C 200). (Figure 15). Oceanic. Cosmopolitan. Common in the plankton (several thousand/1) and in bottom samples in Apalachee Bay. Specimens were usually rather small, averaging 30 microns in diameter. Recorded as common at Beaufort, N.C. and Rockport, Tex.

Genus VII. *Actinocyclus* Ehrenberg

A. ehrenbergii Ralfs. *In* Pritchard, Infusoria, p. 843, 1861. (C 204). (Figure 16). Neritic, littoral, tychopelagic. Eurythermal. Worldwide. This beautiful species was observed from time to time in bottom samples and was present in the plankton in March and February, 1955 in Alligator Harbor. Not reported at Rockport, Tex.

Family HEMIDISCACEAE

Subfamily HEMIDISCOIDEAE

Genus VIII. *Hemidiscus* Wallich

H. hardmanianus (Greville) Mann. Bull. U.S. Nat. Mus., 100:80. (C 200). (Figure 17). Hendey (1937) has grouped all species and varieties of *Hemidiscus* under *H. cuneiformis* Wallich, due to the large number of intermediate forms found by him. The present specimens are quite unlike *H. cuneiformis* in that the fine striae (15–18 in 10 micron) do not meet at the valve center, leaving a large, irregular, hyaline area. The cells frequently failed to separate after division, so that a hemispherical or spherical colony resulted. Valve diameters varied between 100 and 400 microns. Oceanic. Warm water. Observed occasionally in European waters, and Java Sea. In Apalachee Bay infrequent specimens were found 30 miles from shore. No doubt many specimens were destroyed by centrifuging. At Rockport, Tex., it is recorded as occasional at all times of the year. Conger (1954) reports it from the Dry Tortugas area.

Family ACTINODISCACEAE

Subfamily ACTINOPTYCHOIDEAE

Genus IX. *Actinoptychus* Ehrenberg

A. splendens (Shadbolt) Ralfs. *In*: Pritchard, Infusoria, p. 840, 1861. (Figure 18). Neritic and littoral. "Probably an oceanic species" (Hendey, 1937). Temperate species. Possibly tychopelagic. Occasionally in the plankton, fairly common in mud

samples, at Alligator Harbor, Apalachee Bay, Cape San Blas. It is present at both Mobile and Tampa Bay (Cox, 1901).

A. undulatus (Bailey) Ralfs. *In* Pritchard, Infusoria, p. 839, Plate 5, Figure 88, 1861. (C 204). (Figure 19). Neritic, tychopelagic and sometimes planktonic. Euryhaline. Cosmopolitan. Not uncommon but in very small numbers at all times of the year at Alligator Harbor, Cape San Blas, and Apalachee Bay. Present at Beaufort, N.C. and Rockport, Tex.

Suborder AULACODISCINEAE
Family EUPODISCAEAE
Subfamily EUPODISCOIDEAE
GENUS X. *Eupodiscus* RATTRAY

E. radiatus Bailey. Smithson. Contr. Knowl., p. 39, 1850. (C 201, M 103). (Figure 20). This is a large and conspicuous species. It is apparently known only from the Atlantic coast and the northern Gulf of Mexico. Littoral and neritic. Pelagic. Found by the author at Cedar Key, Madiera Beach, Lido Beach, Marco Pass, Alligator Harbor, Apalachee Bay, and Cape San Blas, Fla. In Apalachee Bay it was never absent although the numbers present were never large. The largest concentration was 570 cells/1 in March, 1954 at one station. However, because of its large size it frequently constituted 20 per cent of the phytoplankton volume. It was most abundant in February through May. At Rockport, Tex., it was reported to occur in waters with a salinity range of 21 to 35 ppt. Manly (1953) states that it is "the most abundant disciform diatom on the Carolina coast. Always present in the plankton, frequently dominant." Strangely enough, *Eupodiscus* was not reported from the west coast of Florida by either Davis (1950) or King (1950).

Suborder AULISCINEAE
Family AULISCACEAE
Subfamily AULISCOIDEAE
GENUS XI. *Auliscus* EHRENBERG

A. caelatus Bailey. Smithson. Contr. Knowl., 7:6, Plate 1, Figure 3, 1853. (Figure 21). Neritic and tychopelagic. Warm temperate species. Atlantic and Pacific coasts of U.S. and the Mediterranean. Rare in Apalachee Bay and not common in mud samples.

A. pruinosus Bailey. Smithson. Contr. Knowl., 7:6, Plate 5–8, 1853. (C 201). (Figure 22). Many intermediate forms between this species and *A. punctatus* exist. Neritic. Warm oceans around North America. General distribution poorly known. A few cells were found in Apalachee Bay in May. It is present in small numbers at Beaufort, N.C. (Hustedt, 1955), Tampa and Mobile Bays (Cox, 1901) and Pensacola Bay Boyer, 1926–27).

A. punctatus Bailey. Smithson. Contr. Knowl., 7:6, Plate 1, Figure 9, 1853. (Figure 23). Neritic. Generally distributed in warmer seas. One specimen recorded from Alligator Harbor on a type slide (M 105).

GENUS XII. *Pseudauliscus*

P. radiatus (Bailey) Rattray, J. R. micr. Soc., 8:902, 1888. (C 204). (Figure 24). Littoral and tychopelagic. Eurythermal. Widespread. In North America from New York

to Gulf of Mexico. In the plankton in Apalachee Bay in November, 1954 and March, 1955. Fairly common in sediments.

Suborder BIDDULPHINEAE

Family BIDDULPHIACEAE

Subfamily BIDDULPHOIDEAE

GENUS XIII. *Biddulphia* GRAY

B. alternans (Bailey) Van Heurck. Syn. Diat., p. 208, Plate 21, Figure 644, 1880–1885. (Figure 25). Neritic and littoral. Euryhaline. Cosmopolitan. One specimen found from Apalachee Bay in March, 1954. Common in the plankton at Beaufort, N.C.

B. aurita (Lyngbye) Brébisson and Godey. Consid. sur les Diat., p. 12, 1838. (C 201, M 103). (Figure 26). Neritic and littoral. Cosmopolitan but most widely distributed in cool water. Lebour (1930) says, "Chiefly a spring species (in the North Sea) living near the bottom most of the rest of the year." Very rare in Apalachee Bay. Found November, 1954. Not recorded from elsewhere in the gulf. However, it is recorded as present in all plankton collections at Beaufort, N.C.

B. levis Ehrenberg. Ber. Akad. Wiss. Berl., p. 122, 1844. (C 201). (Figure 27). Neritic and littoral. Euryhaline. Atlantic and Pacific coasts of the United States, northern Europe, Japan, India, and Argentina. A single, empty frustule of this species was found in Apalachee Bay in 1954. It may have been a fossil or from fresh water.

B. mobiliensis Bailey. J. Sci., Amer., 48:336, Plate 4, Figure 24, 1845. (C 204, 203). (Figure 28). Neritic. Temperate and warm-temperate species. Widely distributed in both hemispheres. This distinctive species is rare in numbers in Apalachee Bay but present throughout most of the year, particularly in the fall. In this region it reached 10 cells/1 in shoal waters. My other records show 10 cells/1 at Marco Pass, Fla., October, 1955; 20 cells/1 at Madiera Beach, Fla., December, 1954; and 190 cells/1 at Cedar Key, Fla., October, 1954. Its general occurrence in these waters indicates a preference for low salinity. Conger (1954) quotes an account of very heavy concentrations found at Grand Isle, La., where the salinities are usually low. However, he also mentions an "unaccountable surge" observed at Dry Tortugas, where salinities usually are in the 35–40 ppt range. Conger considers *B. mobiliensis* to be typical of the gulf flora. It has also been recorded at Rockport, Tex. Strangely, it has not been reported from other parts of the west Florida coast.

B. obtusa (Kützing) Ralfs. *In*: Pritchard, Infusoria, p. 848, 1861. (C 201). (Figure 29). Littoral and neritic. Eurythermal. Atlantic and Pacific coasts of North America, Mediterranean, and coasts of Sweden and Finland. A few cells were found in November, 1954 in Apalachee Bay. It has not been reported from elsewhere in the gulf or at Beaufort, N.C.

B. pulchella Gray. Nat. arr. Brit. plants, 1:294, 1821. (Figure 30). Neritic and tychopelagic. Temperate species. Europe, Mediterranean, Atlantic and Pacific coasts of the United States, and India. This species is apparently never abundant. It was found once each at Lido Beach and Marco Pass, Fla., in October, 1954. Presumably it occurs at Apalachee Bay as well. It has been observed at Beaufort, N.C., and Rockport, Tex.

B. rhombus (Ehrenberg) Smith. Syn. Brit. Diat., 2:49, Plate 45, Figure 320, 1856. (C 204). (Figure 31). Neritic and littoral. Eurythermal. Widespread. Although

never very abundant (maximum observed, 110 cells/1 at Marco Pass, Fla.) it was always present in the plankton in Apalachee Bay and along the west coast of Florida. Recorded at Beaufort, N.C., but not at Rockport, Tex.

B. sinensis Greville. J. R. micr. Soc., 14:81, 1866. (M 100). (Figure 32). Neritic and pelagic. Distributed in western Pacific Ocean, Indian Ocean, Red Sea, North Sea, and the coast of Uruguay. The species is of Indo-Pacific origin and first appeared in the North Sea in 1903. It was first reported in the western hemisphere in 1952 at Cape Lookout, N.C. However, J. O. Manly (formerly of Duke University, Dept. of Botany) identified it from a type slide containing Alligator Harbor diatoms collected in 1951. The near simultaneous appearance of this species on the North Carolina coast and in the northern Gulf of Mexico argues for a somewhat earlier arrival in the western hemisphere than 1951. In Apalachee Bay it was noted in very small numbers at irregular intervals in 1954. Not reported at Rockport, Tex.

B. smithii (Ralfs) Van Heurck. Syn. Diat. Belg., p. 207, Plate 105, Figures 1 and 2, 1880–1885. (C 204). (Figure 33). Littoral and tychopelagic. Found once in the plankton in Apalachee Bay, March, 1955.

Genus XIV. *Bellarochia* Van Heurck

B. malleus (Brightwell) Van Heurck. Syn. Diat. Belg., 1880–1885, Figure 142. (C 201). (Figure 34). Neritic and Eurythermal. Widespread but infrequently found. Found only once in Apalachee Bay, during March, 1955, when it was quite common. It has been reported from Cedar Keys, Fla. (Conger unpublished) and in the summer plankton in Beaufort, N.C. It is not reported from Rockport, Tex.

Genus XV. *Corataulina* H. Peragallo *ex* Schütt

C. pelagica (Cleve) Hendey. Disc. Rept., 16:279, 1937. (Figure 35). Neritic. Warm temperate species. Pacific and Atlantic Oceans, Mediterranean, and North Sea. This diatom was present throughout the year, except in winter, in Apalachee Bay. It is an important species, composing 30 per cent of the phytoplankton volume in April, 1954, with secondary maxima in May and October. In October there was an average of 33,000 cells/1. Station analyses show a tendency to bloom in restricted patches, but with no preference for inshore or offshore waters. My records for other Florida waters show 14,000 cells/1 at Panama City, Fla., in December, 1954, 10,000 cells/1 at Marco Pass, Fla. in October and December, 1954. It is not recorded from Rockport, Tex.

Subfamily TRICERATOIDEAE

Genus XVI. *Triceratium* Ehrenberg

T. favus Ehrenberg. Ber. Akad. Wiss. Berl., p. 79, Plate 4, Figure 10, 1840. (Figure 36). Neritic and littoral. Cosmopolitan. Common throughout the year in Alligator Harbor and Apalachee Bay, averaging 15 cells/1. It has been reported as rare throughout the northern Gulf of Mexico.

T. reticulum Ehrenberg. Ber. Akad. Wiss. Berl., p. 127, 1844. (Figure 37). Neritic and littoral. Eurphaline. Cosmopolitan. Occasionally found in the plankton in Apalachee Bay; it is not reported elsewhere in the gulf.

Genus XVII. *Lithodesmium* Ehrenberg

L. undulatum Ehrenberg. Phys. Abh. Akad. Wiss. Berl., p. 75, Plate 4, Figure 13, 1841 b. (M 100, C 201). (Figure 38). Neritic. Warm temperate species. Cosmopolitan. In Apalachee Bay this diatom was present in small numbers in the spring of 1951 and 1954. It is recorded as common at both Rockport, Tex., and Beaufort, N.C.

Subfamily HEMIALOIDEAE

Genus XVIII. *Hemiaulus* Ehrenberg

H. hauckii Grunow. *In*: Van Heurck, Syn. Diat. p. 103, Figure 10, 1880–1885. (C 201). (Figure 39). Neritic. Warm temperate. Cosmopolitan. This was a very important diatom in Apalachee Bay. It appeared in May, 1954 with a concentration of 9,000 cells/1 and lasted into November. The maximum concentration, in July and September, was 19,000 cells/1. The bloom began in inshore waters and maximum numbers occurred in shoal waters. This species is present and occasionally abundant throughout the northern gulf.

H. membranaceous Cleve. Bih. svensk. Vetensk Akad. Handl., 1:6, Plate 1, Figure 5, 1873 b. (C 200). (Figure 40). Probably oceanic. Tropical. In eastern Pacific. Occasionally seen during 1954–1955, in Apalachee Bay with a maximum of 4,000 cells/1 observed in December, 1954. Reported as rare at Rockport, Tex., and not observed at Beaufort, N. C.

H. sinensis Greville. Ann. Mag. Nat. Hist., 16 (591), Plate 5, Figure 9, 1865. (Figure 41). Neritic. Warm temperate species in Atlantic and Pacific Oceans, and the Mediterranean. This species was not as abundant as *H. hauckii*, but had a similar distribution. The maximum number observed was 10,000 cells/1 in May.

Subfamily EUCAMPIOIDEAE

Genus XIX. *Eucampia* Ehrenberg

E. cornuta (Cleve) Grunow. *In*: Van Heurck Syn. Diat., Plate 95, Figure 5, 1885. (Figure 42). Oceanic. Wide distribution in warm waters. In Apalachee Bay, this species has a distribution similar to that of *Hemiaulus*. It occurred in shoal waters from April to October with a maximum of 4,000 cells/1 in September. In inshore waters it was seen from July to September with a maximum of 6,000 cells/1 in July. This species is common in all of the northern gulf.

E. zoodiacus Ehrenberg. Abh. Akad. Wiss. Berl., p. 71, Plate 4, Figure 8, 1840. (M 100, C 200). (Figure 43). Neritic. Warm temperature species. Cosmopolitan. Present occasionally, never abundant in Apalachee Bay. Recorded as common at both Rockport, Tex., and Beaufort, N.C.

Genus XX. *Climacodium* Grunow

C. biconcavum (Ostenfeld) Cleve. Treat. Phytopl. Atl., p. 22, Plate 2, Figures 16 & 17. 1897 b. (Figure 44). Oceanic. Widely distributed in warm waters. In Apalachee Bay this species was found occasionally in the spring in offshore waters. Along the west coast of Florida it occurs well offshore.

Genus XXI. *Streptotheca* Shrubsole

S. themesis Shrubsole. J. Quek. micr. Cl., ser. 2, 4:259, Plate 13, Figures 4, 5, and 6, 1890. (Figure 45). Neritic. Temperate species. West coasts of United States, Europe, and Africa. Found only in February in limited numbers. Not recorded from Rockport, Tex.

Family ANAULACEAE

Subfamily ANAULOIDEAE

Genus XXII. *Terpsinöe* Ehrenberg

T. musica Ehrenberg. Phys. Abh. Akad. Wiss. Berl., Plate 3, 1843. (Figure 46). Littoral and neritic. Euryhaline. Atlantic coast southward to West Indies, Bermuda and off the coasts of Indian and Pacific Oceans. This diatom may be considered typical of the Gulf of Mexico and West Indian flora. It was found sparingly in many plankton samples.

Family CHAETOCERACEAE

Subfamily CHAETOCEROIDEAE

Genus XXIII. *Chactoceros* Ehrenberg

Tabular Key to the Species of *Chaetoceros*

The genus *Chaetoceros* poses a major problem in simple identification. There are about 140 species, many of which look very much alike. Some species have a number of varieties and others can only be separated on the basis of resting spores. There are also seasonal differences within a species.

A dichotomous key to the species of *Chaetoceros* is not generally feasible because of the subtle differences among the morphological characters. Moreover, although the species have been grouped into 16 sections (Gran, 1905; Ostenfeld, 1903; 1913), the criteria used are subject to many exceptions. In order to facilitate identification, the key characters of the species have been arranged in tabular form (Table 1) so that a process of elimination may be used. This method also avoids, to some degree, the possibility of keying a species not included.

Subgenus *Phaeoceros*

Section Atlanticum

Chaetoceros atlanticum Cleve. Bih. svensk. Vetensk. Akad. Handl., 1:11, Plate 2, Figure 8, 1873 a. (C 202). (Figure 47). Oceanic. Cold water. Widespread in northern and southern seas. Found occasionally in December, 1954 in Apalachee Bay. Not reported from Beaufort, N.C. or Rockport, Tex.

C. dichaetum Ehrenberg. Ber. Akad. Wiss. Berl., p. 200, 1845. (Figure 48). Oceanic. Cool temperate species. Cosmopolitan. In Apalachee Bay this diatom was found occasionally in spring at the outermost stations. Not reported previously from the Gulf of Mexico.

TABLE 1

Tabular Key to the Species of *Chaetoceros*

	Figure	μ cell dia.	Chromat. in setae	Process on valve	Term. setae different	Aperature large	Colonial	Spines on all setae	Striae on all spines	Remarks
C. atlanticum	47	10–15	+	+	—	+	+	—	—	
C. dichaetum	48	9–27	+	—	—	+	+	—	—	Setae perpendicular
C. coarctatum	49	30–40	+	—	+	—	+	+	—	to cell axis
C. danicum	50	15	+	—	—	(—)	±	+	—	
C. glandazi	51	15–20	+	*	+	—	+	—	—	Setae swept back
C. peruvianum	52	10–20	+	±	—	....	—	+	+	and diverging.
C. decipiens	53	9–27	—	—	+	‡	+	—	—	Setae fused at
C. lorenzianum	54	9–36	—	—	—	+	+	—	+	base.
C. compressum	55	9–27	—	—	±	±	+	—	—	
C. didymum	56	10–27	—	+	+	+	+	—	—	Deep constric. between
C. constrictum	57	12–36	—	—	—	±	+	—	—	v. and girdle.
C. affinis	58	7–27	—	†	+	—	+	—	—	
C. pelagicum	59	9	—	—	—	+	+	—	—	Some setae fused for
C. diversum	60	9–15	—	—	§	—	+	—	—	2/3 their length.
C. messanense	61	9–12	—	—	+	+	+	—	—	Setae all bent toward
C. curvisetum	62	9–27	—	—	—	+	+	—	—	one side.
C. debile	63	10–36	—	—	—	—	+	—	—	Chains spirally
C. gracile	64	9–12	—	—	—	....	—	—	—	twisted.

* Valves joined by a tube-like process.
† On terminal valves only.
‡ Usually with heavy setae in center of chain, fine setae terminally.
§ Seasonal changes: large in summer.

Section Boreali

C. coarctatum Lauder. J. R. micr. Soc., 12:79, Figure 8, 1864. (C 202). (Figure 49). Oceanic. Widely distributed in warm waters. Found offshore in the spring in Apalachee Bay and in Alligator Harbor in May, but never in large numbers. It is reported from offshore in other portions of the eastern and northern gulf.

C. danicum Cleve. Pelag. Diat. Kattegat, p. 55, 1889. (C 202). (Figure 50). Neritic. Temperate species. Atlantic, Pacific, and Indian Oceans. Present frequently during the year, but never abundant.

C. glandazi Mangin. Bull. Soc. bot. Fr., 57:346, Figure 2, 1910. (C 201). (Figure 51). Oceanic. Warm water. This species is regarded as rare and of limited distribution. Lebour (1930) gives the coast of France (and presumably the North Sea) as its only locale. Hendey (1937) observed it in small numbers off the east coast of Africa and believes it to be a neritic, temperate diatom. In Apalachee Bay, *C. glandazi* was observed in considerable numbers in November, 1954. It is noteworthy that it was not found during routine counting in water mounts, but only in Hyrax mounts. This observation makes it seem probable that the species may be frequently missed when water mounts are used, even at a magnification of 440X. E. M. Hulburt has observed specimens resembling *C. glandazi* in samples from the continental shelf south of Long Island, in the New York Bight. Detailed taxomic investigations are lacking, however.

C. peruvianum Brightwell. Quart. J. micr. Sci., 4:107, Plate 7, Figures 16–18, 1856. (C 203). (Figure 52). Oceanic. Widely distributed in temperate and warm waters. In Apalachee Bay this species was found sparingly in 1953 and 1954 and was abundant in March, 1955. It is reported as rare at Rockport, Tex., and "frequently numerous" at Beaufort, N.C.

Subgenus Hyalochaete

Section Oceanica

Chaetoceros decipiens Cleve. Bih. svensk. Vetensk. Akad. Handl., 1:11, Plate 1, Figure 5, 1873 a. (Figure 53). Oceanic. Considered an arctic and boreal species. However, Cupp (1943) found it in considerable numbers off southern California and Hendey (1937) found "considerable quantities all around the coast of South Africa, in the Brazil Current and in the Peru Current." These are regions of upwelling and the species appear to occur in abundance when cold water appears in warm latitudes in this manner. Cells of the species must be present all the time to take advantage of seasonal temperature changes of this sort, as well as those changes normally associated with summer and winter. This species was very abundant in February, 1954 with a maximum of 200,000 cells/l and virtually disappeared at the end of March. The maximum number is quite large compared to the usual size of bloom populations in this region. It also appears off the west coast of Florida in December. Its unusual distribution, cited above, and the large numbers found in Apalachee Bay make the designations of "arctic" and "tropical" unrealistic. This diatom appears in large numbers in response to cold water, no matter where it occurs geographically. It might be noted that the period during which large numbers are found off the coast of southern California, mid-March through early June, Cupp (1943) coincides with the period of intense upwelling on that coast (Sverdrup *et al.*, 1942), pp. 724–727).

Section Dicladia

C. lorenzianum Grunow. Vehr. zool.-bot. Ges. Wien., 13:157, Plate 5, Figure 13, 1863. (C 203). (Figure 54). Neritic. Temperate and warm waters. Cosmopolitan. This species was always in the plankton and was often the most abundant *Chaetoceros* species. In Apalachee Bay it averaged 14,000 cells/l in March and 110,000 cells/l in July, 1954.

Section Compressa

C. compressum Lauder. J. R. micr. Soc., 12:78, Plate 8, Figure 6, 1864. (M 100) (Figure 55). Neritic. Cool and warm temperate. Rare in Alligator Harbor and Apalachee Bay.

Section Protuberantia

C. didymum Ehrenberg. Ber. Akad. Wiss. Berl., p. 75, 1846. (C 203). (Figure 56). Neritic. Widely distributed in temperate seas. Present in moderate numbers during the entire year, most common in winter. Davis (1950) reports it to be present along the entire west coast of Florida in winter.

Section Constricta

C. constrictum Gran. Den Norske Nordh.-Exped., 1876–1878, p. 17, Plate 1, Figures 11–13, 1897. (M 100). (Figure 57). Neritic. Temperate species. North Atlantic, north Pacific Oceans, and west coast of Africa. Common in Apalachee Bay in November, 1954.

Section Stenocincta

C. affinis Lauder. J.R. micro. Soc., 12:68, Plate 8, Figure 5, 1864. (Figure 58). Neritic. Warm temperate species. North Atlantic coasts of North America, Europe, Mediterranean, and California coast. Common during the summer in Apalachee Bay, never abundant. Common at Rockport, Tex., and Beaufort, N.C.

Section Laciniosa

C. pelagicum Cleve. Bih. svensk. Vetensk. Akad. Handl., 1:11, Plate 1, Figure 4, 1873 a. (Figure 59). Neritic. Temperate species. North Atlantic and Pacific Oceans. Although no cells were found in Apalachee Bay, a few were present in November, 1954, at Panama City, Fla. Not reported at Rockport, Tex.

Section Diversa

C. diversum Cleve. Bih. svensk. Vetensk. Akad. Handl., 1:9, Plate 2, Figure 12, 1873 a. (C 203). (Figure 60). It is uncertain as to whether or not *C. diversum* Cleve and *C. laevia* Leud.-Fort. are the same species. Specimens found in these collections could be referred to either species and many intermediate forms occurred. Since *C. diversum* Cleve has priority all specimens are referred to this species. Neritic. Warm water. In Apalachee Bay this species was not common in 1954, especially inshore. In March, 1955 it was abundant inshore. It is not reported elsewhere in the gulf.

C. messanense Castracane. Atti Accad. 'Nuovi Lincei,' 20:32, Plate 1, Figure 1a, 1875.

(Figure 61). Oceanic. Warm water species. Mediterranean, Southern California coast, Indian Ocean, and west coast of Africa. Present in summer, both inshore and offshore, although never abundant.

Section Curviseta

C. curvisetum Cleve. Pelag. Diat. Kattegat, p. 55, 1889. (Figure 62). Neritic. Coasts of Europe, California, west coast of Africa, Mediterranean, Red Sea, and Labrador. Present in Apalachee Bay in winter, but not common.

C. debile Cleve. Bih. svensk. Vetensk. Akad. Handl., 20:13, pt. 3, Plate 1, Figure 2, 1894. (C 200). (Figure 63). Neritic. Common on all European coasts and coast of California, Arctic Sea, Bering Sea, and Labrador. A few cells were found in March and April, 1955. Not reported from Beaufort, N.C. or other parts of the gulf.

Section Simplicia

C. gracile Schütt. Ber. dtsch. bot. Ges., 13:42, Plate 5, Figure 13, 1895. (Figure 64). Neritic. Eurythermal. Arctic Sea, Baltic Sea, Mediterranean, southern California, and northern North America. Rare in Apalachee Bay. Not recorded from other parts of the gulf.

Suborder SOLENIIDEAE

Family BACTERIASTRACEAE

Subfamily BACTERIASTROIDEAE

Genus XXIV. *Bacteriastrum* Shadbolt

B. delicatulum Cleve. Rep. Fish. Bd. Scotl., pt. 3, p. 298, Figure 16, 1897 a. (C 203). (Figure 65). This species intergrades with *B. varians* Lauder and the latter has been reduced to synonomy (Lebour, 1930). The differences are very slight, being in the sizes of the apertures and terminal state. *B. delicatulum* was considered to be a temperate species whereas *B. varians* was regarded as tropical. In Apalachee Bay, the summer specimens fit the description of *varians* best, but as the water becomes colder gradually they become more like *delicatulum*. Oceanic. Temperate. Eurythermal. Widespread. This diatom was found in the plankton from February through December, 1954. The maximum average count was 26,000 cells/l in July.

B. elongatum Cleve. Treat. Phytopl. Atl., p. 19, Plate 1, Figure 19, 1897 b. (C 203). (Figure 66). Oceanic. Warm water. Widespread. Observed in March, 1955 in small numbers. Present along the west coast of Florida, but not reported at Rockport, Tex., or Beaufort, N.C.

Family RHIZOSOLENIACEAE

Subfamily RHIZOSOLENIOIDEAE

Genus XXV. *Rhizosolenia* (Ehrenberg) Brightwell

Keys to Species of *Rhizosolenia*

1a	Valves tapered symmetrically. Process located on mid-longitudinal axis.	2
1b	Process located excentrically toward valve margin.	3

2a	Valves bluntly rounded with long curved processes. Figure 72.	*R. cylindrus*
2b	Valves cone shaped with a short, hollow process. Figure 69.	*R. bergonii*
3a	Intercalary bands collar-like or ring-shaped; process minute.	4
3b	Intercalary bands scale-like in from two to eight longitudinal rows.	5
3c	Intercalary bands scale-like in many rows.	6
4a	Valves flat, cells curved and joined in spiral chains. Figure 77.	*R. stolterfothii*
4b	Valves acutely tapered; cells sigmoid or crescent shaped. Figure 75.	*R. robusta*
5a	Valve process blunt and tubular; a simple extension of the valve. Figure 68.	*R. alata*
5b	Valve process acute and a distinctly separate structure.	7
6a	Valve conical; process small and pointed; cell wall thick. Figure 67.	*R. acuminata*
6b	Valve blunt; process small and blunt; intercalary bands sculptured and with wavy edges. Figure 71.	*R. castracanei*
7a	When viewed so that spine is displaced to the side, the midline of the intercalary bands are visible. Figure 74.	*R. imbricata*
7b	When viewed as above, the sides but not the midline are visible.	8
8a	Processes thin and extended to form a hair-like spine.	9
8b	Processes stout, pointed and moderately produced.	10
9a	Process thickened for one-quarter to one-half its distance from base, not hollow. Figure 76.	*R. setigera*
9b	Process thickened at base and hollow. Figure 73.	*R. hebetata*
10a	Process straight with small wings at base. Figure 78.	*R. styliformis*
10b	Process curved like a claw; lacks wings at base. Figure 70.	*R. calcar-avis*

R. acuminata (Peragallo). Gran. Diat. Nord. Plankt., p. 50, Figure 59, 1905. (Figure 67). Oceanic. Widely distributed in warm temperate waters. Occurred once in the offshore waters in the spring of 1954. Reported as rare at Rockport, Tex., and abundant at Beaufort, N.C.

R. alata Brighwell. Quart. J. micr. Sci., 6:96, Plate 5, Figure 8, 1858. (C 202). (Figure 68). Oceanic. Temperate and warm waters. This species is the most important diatom in Apalachee Bay and may well be the most important on the west coast of Florida. In number of cells it reaches concentrations in the fall equivalent to the combined *Chaetoceros* populations. In volume it bulks larger than any other species. In September, 1954 the largest average number was 106,000 cells/1. It composed 75 per cent of the phytoplankton volume at that time. A dense population was observed at Marco Pass, Fla. in April, 1955 and was moderately abundant there in October of 1954 (15,000 cells/1). In October, 1954 it reached a maximum of 207,000 cells/1 at Cedar Key, Fla. In Apalachee Bay the cells varied from 3 to 45 micron in diameter and all the customarily described forms were present simultaneously and without regard to distance from shore. On the basis of these collections it appears that the division into forms is an artificial one.

R. bergonii Peragallo. Le Diatomiste 1:110, Plate 15, Figure 15, 1892. (C 202). (Figure 69). Oceanic. Warm water. A few cells observed in Apalachee Bay in December, 1954. It is not previously reported from the gulf.

R. calcar-avis Schultze. Archiv. Anat. Phys. Lpz., p. 339, Plate 13, Figures 1–5, 1858. (C 202). (Figure 70). Oceanic. Warm water. Mediterranean, southern California, Atlantic coast of United States, Java Sea, Japan, and European waters. Found oc-

casionally at all stations in summer. It is moderately common along the west coast of Florida and "fairly common" at Rockport, Tex.

R. castracanei Peragallo. Bull. Soc. Hist. nat. Toulouse, 22:93, Plate 6, Figure 42, 1888. (Figure 71). Oceanic. Warm water. While not found in Apalachee Bay proper, it was observed elsewhere in the gulf.

R. cylindrus Cleve. Treat. phytopl. Atl., p. 24, Plate 2, Figure 12, 1897b. (C 206). (Figure 72). Neritic. Warm water. Widespread, but seldom found. This species was observed in samples taken in March, 1956 at approximately 27° N, 97° W in the northwestern portion of the Gulf of Mexico. It has not been previously reported from the Gulf of Mexico and may not occur in the eastern gulf.

R. hebetata Bailey. Amer. J. Sci, ser. 2, 22: Plate 1, Figures 18 & 19, 1856. (Figure 73). "Semispina" phase. Oceanic. Warm water species. Cosmopolitan. In Apalachee Bay this species was found offshore occasionally in the summer of 1954 and in March, 1955.

R. imbricata Brightwell. Quart. J. micr. Sci., 6:95, Plate 5, Figure 6, 1858. (C 203). (Figure 74). Oceanic. Warm water; seldom in northern European waters. Cosmopolitan. Found in small numbers, irregularly, and mainly in summer. Reported as common the entire year at Rockport, Tex.

R. robusta Norman. *In*: Pritchard, Infusoria, p. 866, Plate 8, Figure 42, 1861. (C 202). (Figure 75). Oceanic. Widespread in warm waters. Present occasionally in Apalachee Bay, but never abundant.

R. setigera Brightwell. Quart. J. micr. Sci., 6:95, Plate 5, Figure 7, 1858. (C 203). (Figure 76). Neritic. Temperate species. Occurred at irregular intervals throughout the year in small numbers. It was common in winter.

R. stolterfothii Peragallo. Bull. Soc. Hist. nat. Toulouse, 22:86, Plate 6, Figure 44, 1888. (M 100). (Figure 77). Neritic. Cosmopolitan. Abundant throughout the year in Apalachee Bay, occasionally very numerous. Three periods of abundance were noted in 1954: the population went from 12,000 cells/l in March to 307,000 cells/l in early May, declined to 10,000 cells/l in late May, rose to 54,000 cells/l in mid-June, declined to 11,000 cells/l in September, and finally increased to 252,000 cells/l in October, falling to 23,000 cells/l in November. No cells could be found by December. These figures are maximum ones and the averages are lower by a third. Because of its large size, *R. stolterfothii* composes a large portion of the phytoplankton biomass, along with *R. alata*. This species is also reported to be abundant along the west coast of Florida and the entire northern gulf.

R. styliformis Brightwell. Quart. J. micr. Sci., 6:95, Plate 5, Figures 5a–d, 1858. (C 200). (Figure 78). Oceanic. Cosmopolitan. Present occasionally in Apalachee Bay in 1953 and 1954 in very small numbers. It is rare at Rockport, Tex. and not reported from Beaufort, N.C.

Genus XXVI. *Guinardia* Peragallo

G. flaccida (Castracane) Peragallo. Le Diatomiste 1:107, Plate 13, Figures 3 & 4, 1892. (M 100). (Figure 79). Neritic. Polyhaline. Warm water species. Cosmopolitan, Present in very small numbers in the fall.

Family LEPTOCYLINDRACEAE

Subfamily LEPTOCYLINDROIDEAE

Genus XXVII. *Leptocylindrus* Cleve

L. danicus Cleve. Pelag. Diat. Kattegat., p. 54, 1889. (Figure 80). Neritic and oceanic. Widespread, sometimes forming large blooms. Most abundant in the spring, averaging 4,800 cells/1 in March, but present at irregular intervals throughout the year. Not previously reported from the gulf.

Family CORETHRONACEAE

Subfamily CORETHRONOIDEAE

Genus XXVIII. *Corethron* Castracane

C. criophylum Castracane. Rept. Challenger, Bot., vol. 2, p. 85, Plate 21, Figure 14, 1886. (C 200). (Figure 81). Hendey (1937) has reduced to synonymy all described species of the genus *Corethron* on the basis that they are all components of a polyphasic species complex, and refers them all to *C. criophylum*. Only one phase, "hystrix" has been found in the Apalachee Bay plankton. Oceanic. Temperate species. Widespread. In very small numbers (10 cells/1) in February and March. Apparently this diatom is present in the entire northern and eastern gulf, but does not form blooms.

Suborder ARAPHIDINEAE

Family FRAGILARIACEAE

Subfamily FRAGILARIODEAE

Genus XXIX. *Asterionella* Hassall

A. japonica Gran. *In*: Nord. Plankton, p. 118, Figure 160, 1905. (Figure 82). Littoral and neritic. Widespread in temperate seas. Most common in winter with an average of 19,000 cells/l in October, 5,000 cells/l in December, and 15,000 cells/l in February. All records were for inshore waters. *Asterionella* is present in moderate amounts throughout the eastern and northern gulf.

Genus XXX. *Synedra* Ehrenberg

S. fulgens (Greville). W. Smith. Syn. Brit. Diat., 1:74, Plate 12, Figure 103, 1853. (Figure 83). Littoral. Occasional specimens were seen on permanent slides.

Genus XXXI. *Thalassiothrix* Cleve and Grunow

T. frauenfeldii Grunow. *In*: Cleve & Grunow. Bih. svensk. Vetensk. Akad. Handl., 17:109, 1880. (C 203). (Figure 84). Oceanic. Warm temperate species. Widespread. Present throughout the year, but most common in winter. The highest density found was 10,000 cells/l in shoal water in February. In other localities, maxima of 33,300 cells/1 were found in December at Panama City, Fla. and 5,000 cells/1 at Marco Pass, Fla. This species is common along all the gulf coast.

T. mediterranea Pavillard. Rech. Diat. pelag. Golfe du Lion, p. 39, Plate 2, Figure 3,

1916. (C 203). (Figure 85). Oceanic. Temperate and warm temperate. Widespread. In Apalachee Bay this diatom occurred only during March and April in small numbers (500–1,600 cells/1). At Panama City, Fla. it reached a density of 7,000 cells/1.

Genus XXXII. *Thalassionema* (Grunow) Hustedt

T. nitzshioides Hustedt. *In:* Rabenhorst's Kryptogamenflora, pt. 2, p. 244, Figure 725, 1932. (C 203). (Figure 86). Present throughout the year in Apalachee Bay and common elsewhere in the gulf. The greatest concentration observed was 65,000 cells/1 in October, 1954. Because of its small size, it is an unimportant constituent of the plankton.

Genus XXXIII. *Campylosira* Grunow

C. cymbelliformis (A. Schmidt) Grunow. *In*: Van Heurck, Syn. Diat., Plate 45, Figure 43, 1880–1885. (C 201). (Figure 87). Littoral and tychopelagic. Temperate species. Cosmopolitan. Found in November, 1954, inshore, and is reported as occasional at Rockport, Tex.

Genus XXXIV. *Dimerogramma* Ralfs

D. sp. (C 204). A single frustule was found in a permanent mount made from a collection in March, 1955. The genus is decidedly rare, at least in the plankton.

Genus XXXV. *Plagiogramma* Greville

P. inaequale Greville. Quart. J. micr. Soc., 7:210, Plate 10, Figure 10, 1859. (C 201). Littoral and tychopelagic. Warm water. West Indies, Honduras, and Campeche Bay. In plankton samples from Apalachee Bay in November, 1954.

P. tesselatum Greville. Quart. J. micr. Soc., 7:208, Plate 10, Figure 7, 1859. (C 204). (Figure 88). Littoral and tychopelagic. Warm water. Frequently found in samples from Alligator Harbor in 1955.

Family TABELLARIACEAE

Subfamily TABELLARIOIDEAE

Genus XXXVI. *Licmophora* Agardh

L. abbreviata Agardh. Consp. Crit. Diat., p. 42, 1831. (Figure 89). Littoral and tychopelagic. Widespread. Baltic Sea, Atlantic coast of United States, Puerto Rico, Mediterranean, and India. Rare in the plankton but 3,000 cells/1 were found in March, 1954. Widely reported in the gulf and Atlantic coasts.

Genus XXXVII. *Rhabdonema* Kützing

R. adriaticum Kützing. Bacill. Plate 18, Figure 7, 1844. (M 105). (Figure 24), 1844. (C 204). (Figure 91). Littoral and tychopelagic. Warm water species. Cosmopolitan. Occasional single cells found in Apalachee Bay and other portions of the Florida coast.

Genus XXXIX. *Striatella* Agardh

S. interrupta (Ehrenberg) Heiberg. Consp. Diat., p. 73, Plate 5, Figure 15, 1863. (Figure 92). Neritic and littoral. Cold water. Northern European and Atlantic coasts.

Very rare in Apalachee Bay, a few specimens found in September, 1954. Not previously recorded from the gulf.

S. unipunctata (Lyngbye) Agardh. Consp. Crit., Diat., p. 60, 1832. (Figure 93). Littoral and tychopelagic. Temperate species. Occasionally present in the plankton on the gulf coasts.

Suborder MONORAPHIDINEAE

Family ACHNANTHACEAE

Subfamily ACHNANTHOIDEAE

GENUS XL. *Achnanthes* BORY

A. manifera Brun. Le Diatomiste 2, Plate 16, 1895. (M 100). Littoral. Hypohaline. Tropical and sub-tropical. (Hustedt, 1955). A single specimen noted on a permanent slide.

GENUS XLI. *Cocconeis* EHRENBERG

C. disculoides Hustedt. Bull. Duke Univ. Mar. Sta., 6, Plate 5, Figures 8–11, 1955. (C 205). Littoral and tychopelagic. Heretofore reported only from type locality: Beaufort, N.C. (Hustedt, 1955). While reported to be common at Beaufort, only one frustule was found in September, 1954, in Apalachee Bay plankton.

C. scutellum Ehrenberg. Infus., p. 194, Plate 14, Figure 8, 1838. (Figure 94). Neritic and tychopelagic. Common in all seas. Although rare in the plankton this diatom is common in the bottom sediments. Not reported from elsewhere in the gulf, but found by Conger at Cedar Keys, Fla., in 1949 (unpublished list).

Suborder BIRAPHYDINEAE

Family NAVICULAECEAE

Subfamily NAVICULOIDEAE

GENUS XLII. *Navicula* BORY

Navicula sp. A large number of unidentified species were observed in the plankton, but their contribution is so small in terms of biomass, that they were not customarily enumerated. However, permanent slides containing such specimens were prepared and are available for detailed study.

GENUS XLIII. *Pleurosigma* W. SMITH

P. decorum W. Smith. Syn. Brit. Diat., 1:63, Plate 21, Figure 196, 1853. (C 204). (Figure 95). Littoral and tychopelagic. Temperate species. Rare in the plankton; occasional in the sediments.

GENUS XLIV. *Gryosigma* HASSALL

G. balticum (Ehrenberg) Cleve. Bih. svensk. Vetensk. Akad. Handl., 26:118, 1894–1895. (C 204). (Figure 96). Littoral, neritic, and tychopelagic. Both coasts of the United States, northern European waters, India, Japan, and Mediterranean. Occasional in the plankton; never abundant.

Genus XLV. *Trachyneis* Cleve

T. aspera (Ehrenberg) Cleve. Bih. svensk. Vetensk. Akad. Handl., 26:191, 1894–1895. (C 205). Littoral and tychopelagic. Cosmopolitan. Observed in the plankton in Apalachee Bay in September, 1954; rare.

Subfamily AMPHIPROROIDEAE

Genus XLVI. *Tropidoneis* Cleve

T. lepidoptera (Gregory) Cleve. Bih. svensk. Vetensk. Akad. Handl., 26:25, 1894–1895. (Figure 97). Littoral and tychopelagic. Temperate species. Widespread. Occasional in the plankton at all stations, in summer. This species is typical of many similar ones that are common on mud flats and occur in the plankton regularly, although it is not their normal habitat.

T. maxima (Gregory) Cleve. Bih. svensk. Vetensk. Akad. Handl., 26:26, 1894–1895. (Figure 98). Littoral, neritic, and tychopelagic. Widespread. Rare in the plankton in Apalachee Bay.

Family CYMBELLACEAE

Subfamily CYMBELLOIDEAE

Genus XLVII. *Amphora* Ehrenberg

A. arenaria Donkin. J. R. micro. Soc. Lond., 6:3. Plate 13, Figure 16, 1858. (Figure 99). Littoral and tychopelagic. Cosmopolitan. Occasional in the plankton.

A. micans Schmidt. Atlas, Plate 26, Figure 18, 1875. (M 105). Neritic. Previously known only from type locality: Campeche Bay. One specimen from Alligator Harbor on type slide.

A. sulcata Schmidt. Atlas, Plate 26, Figures 46 & 47, 1875. (C 204). Littoral and tychopelagic. Mediterranean and Caribbean. A few frustules observed occasionally in the plankton; more abundant in bottom sediments. Not reported at Rockport, Tex. or Beaufort, N. C.

A. marina W. Smith. (Tentative). (C 200).

Family BACILLARIACEAE

Subfamily NITZSCHIOIDEAE

Genus XLVIII. *Nitzschia* Hassall

N. closterium (Ehrenberg) W. Smith. Syn. Brit. Diat., 1:42, Plate 15, Figure 120, 1853. (Figure 100). Neritic. Cosmopolitan. *Nitzschia closterium* is one of the few diatoms to be found in the plankton at all seasons, regardless of distance from shore or depth of sample. In the winter, it is frequently the only species taken.

N. insignis Gregory. J. R. micr. Soc. Lond., 5:80, Plate 1, Figure 57, 1857. (C 204). (Figure 101). Neritic. Temperate species. From Alligator Harbor in March, 1955.

N. longissima (Brébisson) Ralfs. *In*: Cleve and Grunow. Bih. svensk. Vetensk. Akad. Handl., 17:100, 1880. (C 201). (Figure 102). Littoral. Cosmopolitan. Present throughout the year in small numbers in Apalachee Bay. Common in November, 1955.

N. paradoxa (Gmelin) Grunow. *In*: Van Heurck Syn. Diat., p. 176, Plate 61, Figure 6, 1880. (C 201). (Figure 103). Littoral. Euryhaline. Cosmopolitan. Rare in the plankton, although abundant on mud flats and in estuaries.

N. pungens var. *atlantica* Cleve. Treat. phytopl. Atl., p. 24, Plate 2, Figure 24, 1897b. (C 201). (Figure 104). Neritic. Temperate species. Several cells found in Hyrax mounts from samples taken in November, 1954. This species may be more abundant than deduced from routine counts with water mounts.

N. seriata Cleve. Vega-Exp. Sakttag., 3:478. 1883. (Figure 105). Neritic. Cool temperate. Widespread in northern and southern hemisphere. The most abundant *Nitzschia* in the region. Always present and occasionally in fairly large numbers, particularly in winter, seldom less than a thousand per liter. It averaged 47,000 cells/1 in October, 1954.

Suborder SURIRELLINEAE

Family SURIRELLACEAE

Subfamily SURIRELLOIDEAE

GENUS XLIX. *Surirella* TURPIN

S. fastuosa Ehrenberg. Ber. Phys. Abh. Akad. Wiss. Berl., 19:214, 1840. (Figure 106). Neritic and tychopelagic. Polyhaline. Warm water. Occasional in the plankton. Recorded as rare at Rockport, Tex.

Subfamily CAMPYLODISCOIDEAE

GENUS L. *Campylodiscus* EHRENBERG

C. punctulatus (Grunow) *In*: A. Schmidt, Atlas, Plate 17, Figure 4, 1875. (C 204). (Figure 107). Neritic and tychopelagic. Warm water. Hitherto known only from the type locality: Campeche Bay, and considered to be rare (Boyer, 1927).

C. samoensis Grun. *In*: A. Schmidt, Atlas, Plate 15, 1875. (C 200). (Figure 108). Neritic. Warm water. Vera Cruz, Mexico, and Mediterranean. One specimen on a type slide from a collection made December, 1954.

Dinoflagellates

Dinoflagellates are second in importance only to the diatoms as primary producers of organic matter in the oceans. They never approach the diatoms in total numbers of biomass except in a few localities and for limited periods. The largest count recorded by Gran (1915) in the North Sea for *Ceratium tripos* was 3,740 cells/1. In certain coastal regions such as the west coast of Florida large blooms of upwards of several million organisms may be found. Although only a few cells may be present, many dinoflagellate species are important on account of their large size. For example, the average *Ceratium tripos* cell found in Apalachee Bay has a volume of 240,000 cubic micra, which is somewhat more than that of a large *Biddulphia mobiliensis*. The largest diatoms, such as *Rhizosolenia*, are frequently far more abundant than any of the dinoflagellates of comparable size and volume.

The dinoflagellates of the Gulf of Mexico are not well known. The state of our ignorance has been ably summarized by Graham (1954). In addition, to reviewing the work done up to that date, he also presents some previously unpublished data of other workers. He lists a total of 26 species known to exist in the gulf. It should be emphasized that a careful investigation of unarmored species would undoubtedly produce a much larger list.

In this investigation a total of 8 genera and 17 species were enumerated. The remarks on distribution and temperature made with reference to diatoms apply equally well to the Pyrrophyta.

The most common and abundant dinoflagellate in Apalachee Bay was *Ceratium furca.* It is typical of the local plankton but primarily because of its apparently simple requirements. If any dinoflagellate was to be regarded as characteristic, on the basis of this cursory study it would be *Podolampas elegans* Schütt.

The taxonomic scheme of Melchior (1954) has been used. The names used are those found in Wood (1954) and Lebour (1925). Wood (1954) gives complete synonymy for many species listed here.

Artificial Keys to the Dinoflagellates

The remarks concerning the use of keys, made in connection with the key to the diatoms, are equally pertinent here. Dinoflagellates have a complex external structure and a difficult terminology associated with it.

Usually with a transverse furrow and flagellum; cellulose plates frequently present; usually with brownish or olive green chloroplasts. 1

1a Cells naked. Figure 112. *Gymmodinium*
1b Cells with a rigid wall composed of plates. 2
2a Cells rounded or pointed lacking girdle and sulca; with two flagella at apical end; theca of two longitudinally divided halves. 3
2b Cells with girdle and sulcus (sometimes not apparent) ; flagella from a median pore; covered with a theca of from one to five plates. Cells not colonial, longitudinal axis longer; equal or only slightly shorter than transverse axis. 4
3a Cell rounded. *Exuviaella*
3b Cell with an apical spine and the antapical end terminating in a point. *Prorocentrum*
4a Theca formed of three pairs of symmetrical plates; epitheca very small, girdle situated at the apical end and winged; cell laterally compressed with a longitudinal wing. Figures 110 & 111. *Dinophysis*
4b Cell spindle-shaped, both ends pointed; theca divided longitudinally into ridges; girdle in the upper third of the cell. Figure 124. *Oxytoxum*
4c Theca divided into numerous plates; a girdle, when present, dividing the cell into equal halves. 5
5a Girdle not apparent; cell pear-shaped; apical horn with a pore; hypocone with one or two winged spines; theca thin. Figure 125. *Podolampas*
5b Girdle well developed; theca strongly developed. 6
6a Apical end produced to form a long tubular spine; the hypocone with one to three tubular spines, the latter sometimes reflexed; the sulcus is a flat plate. Figures 115 to 123. *Ceratium*
6b Cells spherical, pear-shaped or flattened; apical end conical; antapical conical, rounded or with one or more short spines. 7
7a Girdle ends displaced vertically at sulcus, sometimes overlapping; theca heavily ornamented. Figure 114. *Goniaulax*
7b Girdle ends not displaced; theca with little or no ornamentation, usually smoothly rounded. Figure 113. *Peridinium*

Order PROROCENTRALES

GENUS I. *Exuviella* CIENKOWSKI

E. compressa (Bailey) Ostenfeld. (Figure 109). Oceanic. All oceans. A few cells found in the summer plankton in Apalachee Bay. At Marco Pass, Fla. it was found in small numbers in October, 1955.

Order DINOPHYSALIDALES

Family DINOPHYSALIDACEAE

GENUS II. *Dinophysis* EHRENBERG

D. caudata Saville-Kent. (C 202). (Figure 110). Neritic. Tropical to warm temperate seas. Widely distributed. Present only in the spring in Apalachee Bay. Occasional samples contained 10 cells/1, both inshore and offshore. The densest populations were found at Cedar Key, Fla. in October, 1954, with 65 cells/1.

D. tripos Gourret. (Figure 111). Oceanic and euryhaline. Warm water. Atlantic Ocean (Gulf Stream) to Norway and Greenland, perennial in Mediterranean, Australia, California, and Cape Horn. Rare in Apalachee Bay and along west coast of Florida.

Order GYMNODINIALES

Family GYMNODINIACEAE

GENUS III. *Gymnodinium* STEIN

G. brevis Davis. (Figure 112). Neritic and estuarine. Warm water species. The type locality is an area extending from Key West, Fla., north to Tarpon Springs, and extending to 30 miles from shore. It has also been reported from lagoons on the Texas coast. No specimens were found in Apalachee Bay. In December, 1955, there were 288,000 cells/1 at Marco Pass, 45,000 cells/1 at Lido Beach. In 1954 and 1955 no specimens were found north of Madiera Beach.

Order PERIDINIALES

Family PERIDINIACEAE

GENUS IV. *Peridinium* EHRENBERG

P. depressum Bailey. (Figure 113). Oceanic. Eurythermal and euryhaline. Worldwide. Present throughout the year, but most common in the spring with an average density of 15 cells/1 falling to a density of 3 cells/1 the remainder of the year. The largest population observed was 120 cells/1 in July.

Family GONIAULACEAE

GENUS V. *Goniaulax* DIESING

Goniaulax sp. (C 203). (Figure 114). Many very small specimens were observed but have not been identified to species.

Family CERATIACEAE

GENUS VI. *Ceratium* SCHRANK

C. furca (Ehrenberg) Claparede & Lachmann. (C 201). (Figure 115). Neritic and euryhaline. Cosmopolitan. This is the most abundant dinoflagellate in these waters,

as well as the most common. It is most numerous in the spring and fall. Densities ranged from a high of 58 cells/1 in March to 2 cells/1 during summer, to a second high of 70 cells/1 in October. Individual samples frequently showed much larger numbers, *e.g.*, 160 cells/1 on March 5 in a "tide line" five miles from shore.

C. fusus (Ehrenberg) Dujardin. (Figure 116). Neritic and eurythermal. Widespread in all oceans. Present irregularly throughout the year. Periods of abundance in 1954 were: February–March, 12 cells/1; June–July, 34 cells/1; September, 20 cells/1; October–December, 10 cells/1. It was absent at other times. This species is common along the Florida west coast.

C. gibberum Gourret. (Figure 117). Oceanic. In all oceans when temperature is above 20°C. Found only once, in March, 1954, in Apalachee Bay.

C. macroceros (Ehrenberg) Cleve. (C 201). (Figure 118). Oceanic. Cool and warm temperate species. All oceans. Present sporadically from July to December. Never abundant. Present along entire Florida west coast.

C. massiliense (Gourret) Jørgensen. (Figure 119). Littoral and neritic. Warm temperate species. Widely distributed. Present only in late February and early March, about 10 cells/1.

C. pentagonum Gourret. (Figure 120). Oceanic. Eurythermal. All oceans. Found only in samples taken inshore at Panama City in the fall of 1954.

C. pulchellum Schroeder. (Figure 121). Oceanic. Stenohaline. Temperate and warm water species. Widely distributed. Found once in Apalachee Bay in March, 1954.

C. trichoceros (Ehrenberg) Kofoid. (Figure 122). Oceanic. Warm water. In Atlantic from 28° S. to northern end of Florida Current, Mediterranean, and Pacific Ocean. A few specimens present in the spring in Apalachee Bay. Present along the west coast of Florida.

C. tripos var. *atlanticum* Ostenfeld. (C 203). (Figure 123). Oceanic. Abundant in temperate and warm seas. Common in February–March and again in May–December, 1954. The most dense population observed occurred in March, averaging 18 cells/1. Common along the west coast of Florida.

Family OXYTOXACEAE

Genus VII. *Oxytoxum* Stein

O. scolopax Stein. (Figure 124). Oceanic. Warm water. All oceans. One specimen from Apalachee Bay, found 30 miles offshore in July, 1954.

Family PODOLAMPACEAE

Genus VIII. *Podolampas* Stein

P. elegans Schütt. (Figure 125). This is a striking but relatively rare species of *Podolampas*. It has been reported from the Mediterranean by Lohmann (1902), from the Red Sea by Schroeder (1906), and from the Atlantic Ocean by Karsten (1906). It is very small and transparent and would escape fine plankton nets and be overlooked when caught. Considering its reputed scarcity, it was a surprisingly common member of the plankton. *Podolampas* was present during all of March with an average of 3 cells/1, and a maximum of 30 cells/1 at some inshore stations. It was then absent until July and was then present every month thereafter with an average density of 3 cells/1.

Coccolithophores and Silicoflagellates

Neither of these groups appeared to be important constituents of the plankton of the northeastern Gulf of Mexico. In general, coccolithophores are abundant in the tropics and in such localities as the Mediterranean Sea in particular (Bernard, 1948). Centrifuged samples from the west and north coasts of Florida did not reveal the presence of a coccolith flora. One specimen of a coccolith was found during 1954. Davis (1950) records coccolithophores as being present at Rock Island, Fla. in December, 1947. *Pontosphaerea* sp. was tentatively identified from a sample taken in August, 1953, in Alligator Harbor. Silicoflagellates are somewhat more abundant in this region. Davis (1950) records them from Ft. Myers, Anclote Light, and Rock Island in December, 1947. In 1954 and 1955 they were found in some abundance at Marco Pass, Fla. (*Dichtyocha fibula* var. *messanensis* (Haekel) Lemmermann) and occasionally in Apalachee Bay, (*Ebria tripartita* (Schumann) Lemmermann).

Cyanophyta

With the exception of a few references to blooms of *Trichodesmium sp.* (Taylor, 1928; King, 1950) and notice of a few other genera, the presence of planktonic blue-green algae in the Gulf of Mexico has been largely ignored.

Several different kinds of blue-greens were noted during 1954 and 1955. *Trichodesmium thiebauti* Gomont was found occasionally but never in abundance. Only one bloom of this species was noted. On November 19, 1954 a fine yellow-green "dust" was noted floating on the surface about 10 miles south of Alligator Harbor. Samples taken a few feet beneath the surface did not yield any cells, however. It has been suggested that *Trichodesmium erythreum* may grow on the bottom and rise to the surface only under special conditions (Feldmann, 1932), but bottom samples from this locality have not revealed its presence. *Trichodesmium erythreum* is found extensively in the western gulf.

Two other forms were noted from time to time in the samples. One, fairly common during the summer, appeared to be one of the Chroococaceae and bore a resemblance to *Gomphosphaeria.* The other, less common, had a monifiliform appearance and appeared to be a member of the Nostocaceae. None of the specimens possessed heterocysts or akinetes. There are several genera with this growth form (*Iocystis, Pseudoanabaena*), but their taxonomic status is in doubt (Fritsch, 1952, p. 835). The numbers of cells of blue-green algae found in Apalachee Bay during 1954 were: July 28, 30, 940 cells/l; October 1, 71,000 cells/l; October 14, 48,000 cells/l; and October 29, 273,000 cells/l.

Summary

1. Routine phytoplankton collections were made from November, 1953 to July, 1955 in Apalachee Bay in the northeastern Gulf of Mexico, and along the west coast of Florida. Samples consisted of one liter of water concentrated in a Foerst centrifuge.
2. A total of 116 species of diatoms, grouped into 50 genera, were found. Thirty diatom genera were represented by only one species. The genera *Rhizosolenia* (12 species) and *Chaetoceros* (18 species) included between 8 and 65 per cent of the individuals

found in any one sample in 1954. *Rhizosolenia alata* Brightwell was the most abundant summer species and *Chaetoceros decipiens* Cleve was the most abundant winter species.

3. The designations "arctic" and "tropical" are untenable when applied to plankton diatoms since the occurrence of many species is determined by seasonal temperature changes.
4. Twenty-three species of diatoms are reported from the Gulf of Mexico for the first time. Three of these were known only from the type locality.
5. Seventeen dinoflagellate species were found. *Ceratium furca* (Ehrenberg) Clap. and Lach. was the most common and abundant dinoflagellate. *Podolampas elegans* Schütt was a very characteristic species and was surprisingly abundant.
6. One coccolithophore, *Pontosphaerea sp.*, one blue-green alga, *Trichodesmium thiebauti* Gomont, and two silicoflagellates, *Dichtyocha fibula* var. *messanensis* (Haekel) Lemmermann and *Ebria tripartita* (Schumann) Lemmermann, were found.

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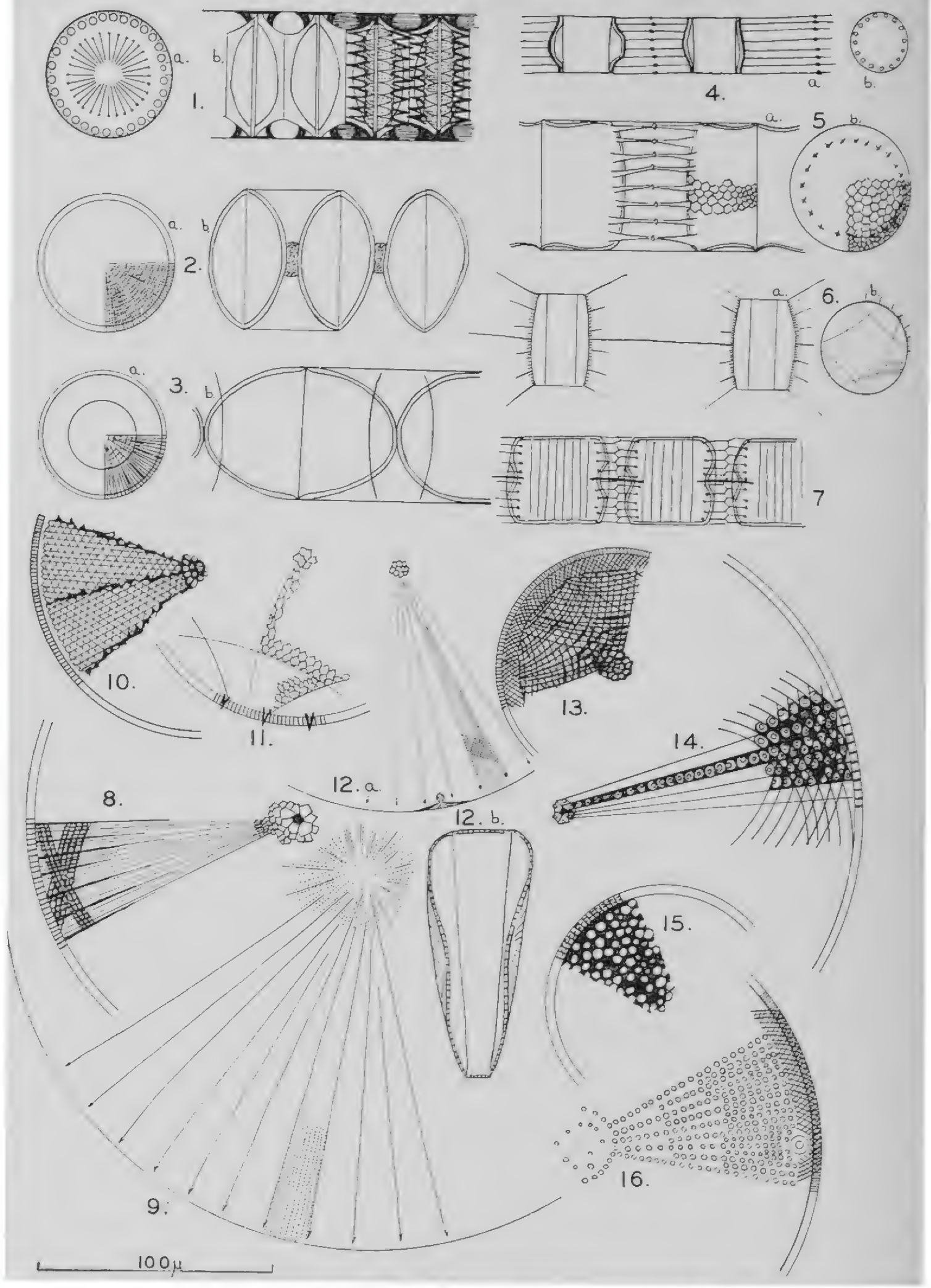


FIG. 1–16. 1. *Melosira sulcata* (Ehrenberg) Kützing, a. valve, b. girdle; 2. *Melosira dubia* Kützing, a. valve, b. girdle; 3. *Melosira nummuloides* (Lyngbye) Agardh, a. valve, b. girdle; 4. *Skeletonema costatum* (Greville) Cleve, a. girdle, b. valve; 5. *Stephanopyxis palmeriana* (Greville) Grunow, a. girdle, b. valve; 6. *Thalassiosira decipiens* (Grunow) Jørgensen, a. girdle, b. valve; 7. *Schroederella delicatula* (Peragallo) Pavillard, girdle; 8. *Coscinodiscus centralis* Ehrenberg, valve; 9. *Coscinodiscus concinnus* Wm. Smith, valve; 10. *Coscinodiscus denarius* A. Schmidt, valve; 11. *Coscinodiscus excentricus* Ehrenberg, valve; 12. *Coscinodiscus granii* Gough, a. valve, b. girdle; 13. *Coscinodiscus kutzingii* A. Schmidt, valve; 14. *Coscinodiscus oculus iridis* Ehrenberg, valve; 15. *Coscinodiscus radiatus* Ehrenberg, valve; 16. *Actinocyclus ehrenbergii* Ralfs, valve.

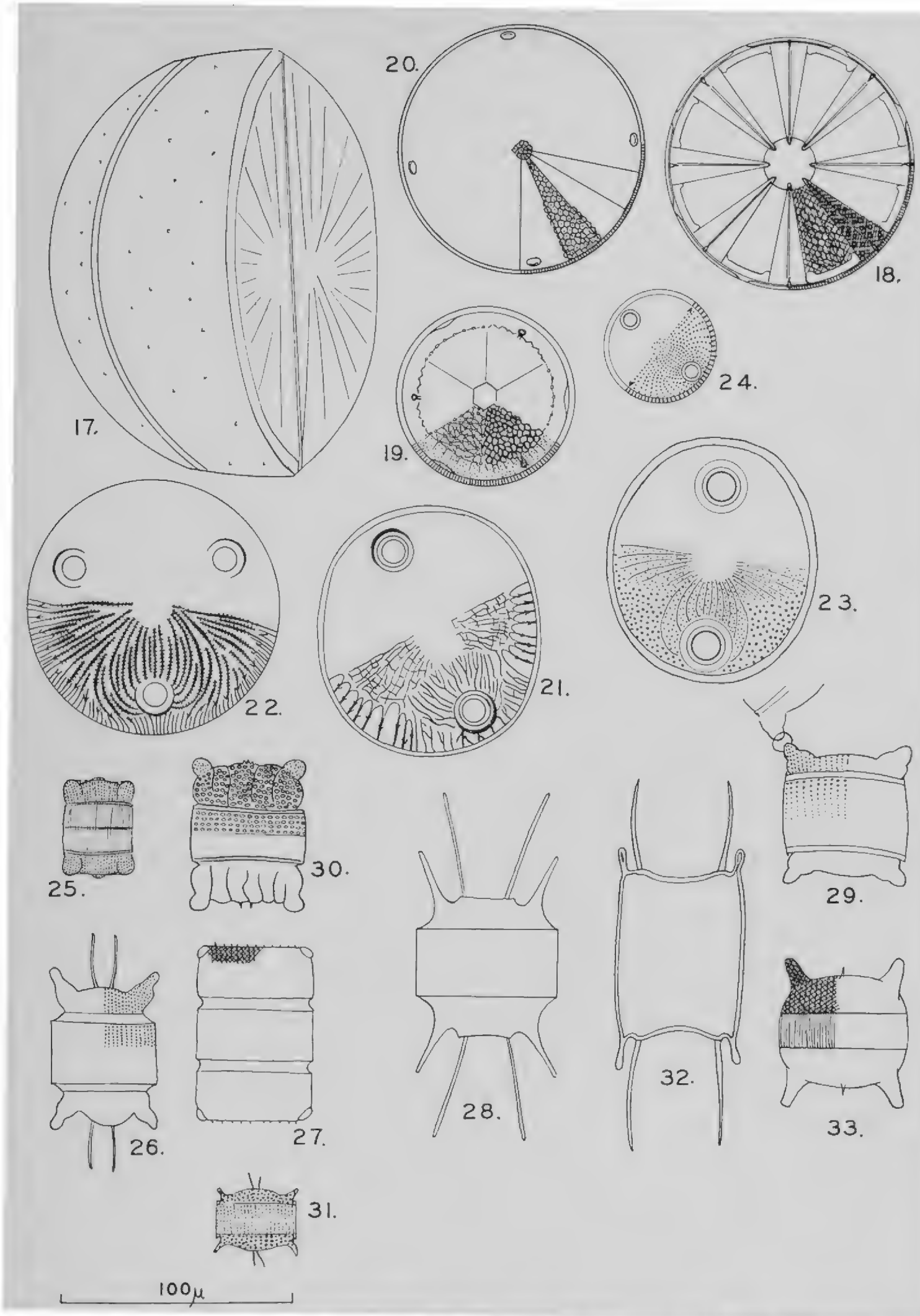


FIG. 17–33. 17. *Hemidiscus hardmanianus* (Greville) Mann, girdle and valve; 18. *Actinoptychus splendens* (Shadbolt) Ralfs, valve; 19. *Actinoptychus undulatus* (Bailey) Ralfs, valve; 20. *Eupodiscus radiatus* Bailey, valve; 21. *Auliscus caelatus* Bailey, valve; 22. *Auliscus pruinosus* Bailey, valve; 23. *Auliscus punctatus* Bailey, valve; 24. *Pseudauliscus radiatus* (Bailey) Rattray, valve; 25. *Biddulphia alternans* (Bailey) Van Heurck, girdle; 26. *Biddulphia aurita* (Lyngbye) Brébisson & Godey, girdle; 27. *Biddulphia levis* Ehrenberg, girdle; 28. *Biddulphia mobiliensis* Bailey, girdle; 29. *Biddulphia obtusa* (Kützing) Ralfs, girdle; 30. *Biddulphia pulchella* Gray, girdle; 31. *Biddulphia rhombus* (Ehrenberg) W. Smith, girdle; 32. *Biddulphia sinensis* Greville, girdle; 33. *Biddulphia smithii* (Ralfs) Van Heurck, girdle.

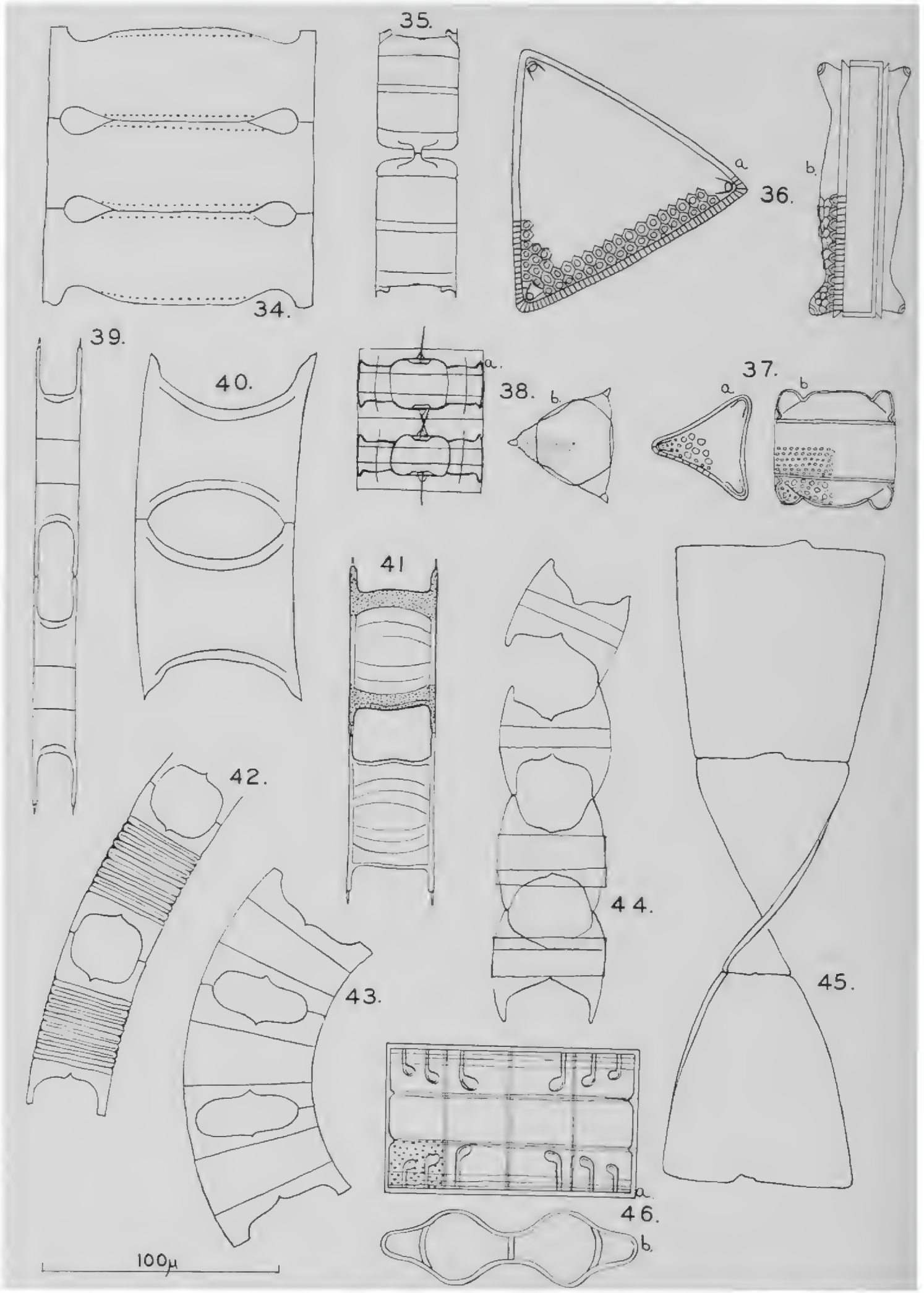


FIG. 34–46. 34. *Bellarochia malleus* (Brightwell) Van Heurck, girdle; 35. *Cerataulina pelagica* (Cleve) Hendey, girdle; 36. *Triceratium favus* Ehrenberg, a. valve, b. girdle; 37. *Triceratium reticulum* Ehrenberg, a. valve, b. girdle; 38. *Lithodesmium undulatum* Ehrenberg, a. girdle, b. valve; 39. *Hemiaulus hauckii* Grunow, girdle; 40. *Hemiaulus membranaceous* Cleve, girdle; 41. *Hemiaulus sinsensis* Greville, girdle; 42. *Eucampia cornuta* (Cleve) Grunow, girdle; 43. *Eucampia zoodiacus* Ehrenberg, girdle; 44. *Climacodium biconcavum* (Ostenfeld) Cleve, girdle; 45. *Streptotheca themesis* Shrubsole, girdle; 46. *Terpsinöe musica* Ehrenberg, a. girdle, b. valve.

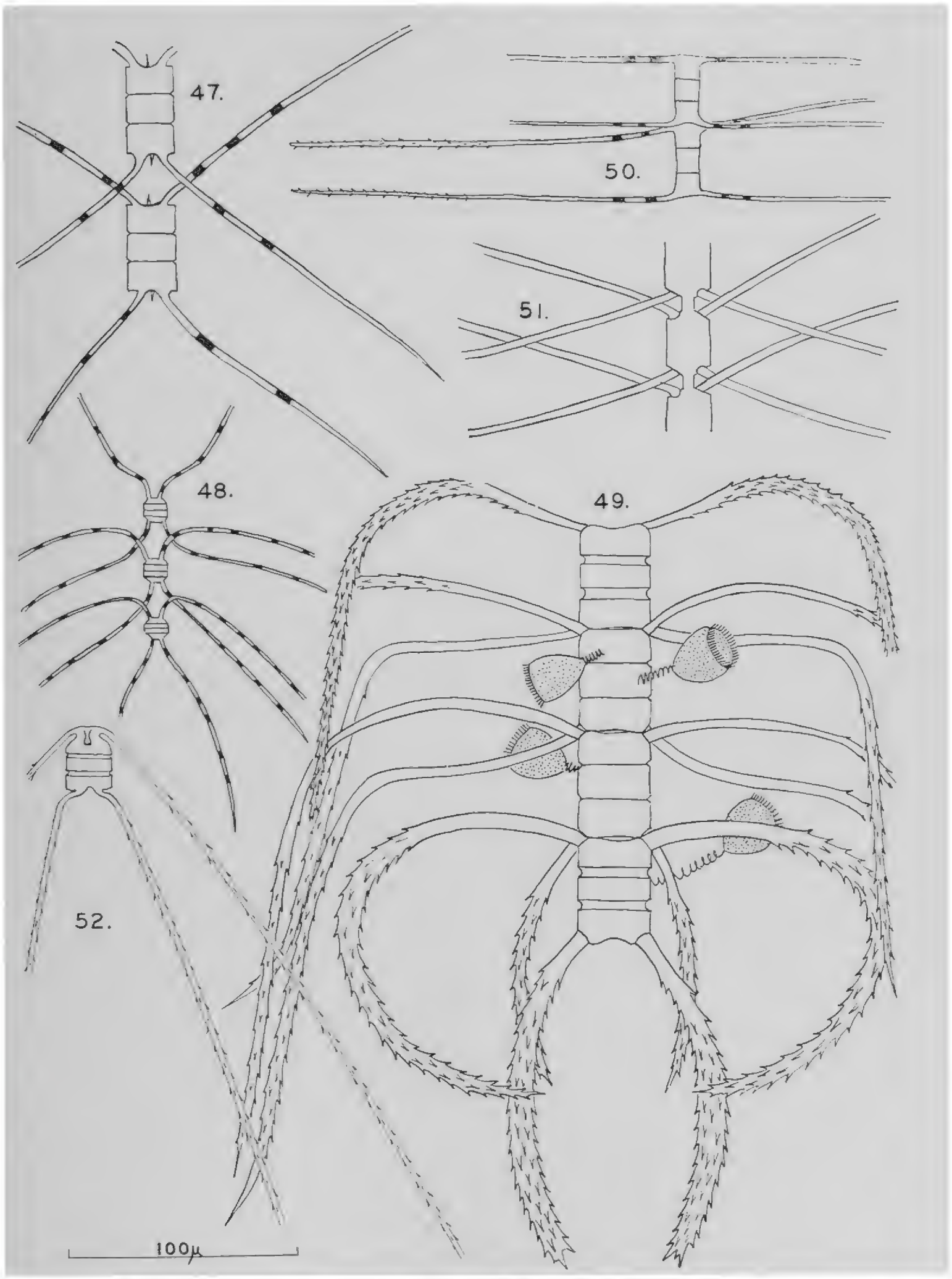


FIG. 47–52. 47. *Chaetoceros atlanticum* Cleve, girdle; 48. *Chaetoceros dichaetum* Ehrenberg, girdle; 49. *Chaetoceros coarctatum* Lauder, girdle; 50. *Chaetoceros danicum* Cleve, girdle; 51. *Chaetoceros glandazi* Mangin, girdle; 52. *Chaetoceros peruvianum* Brightwell, girdle.

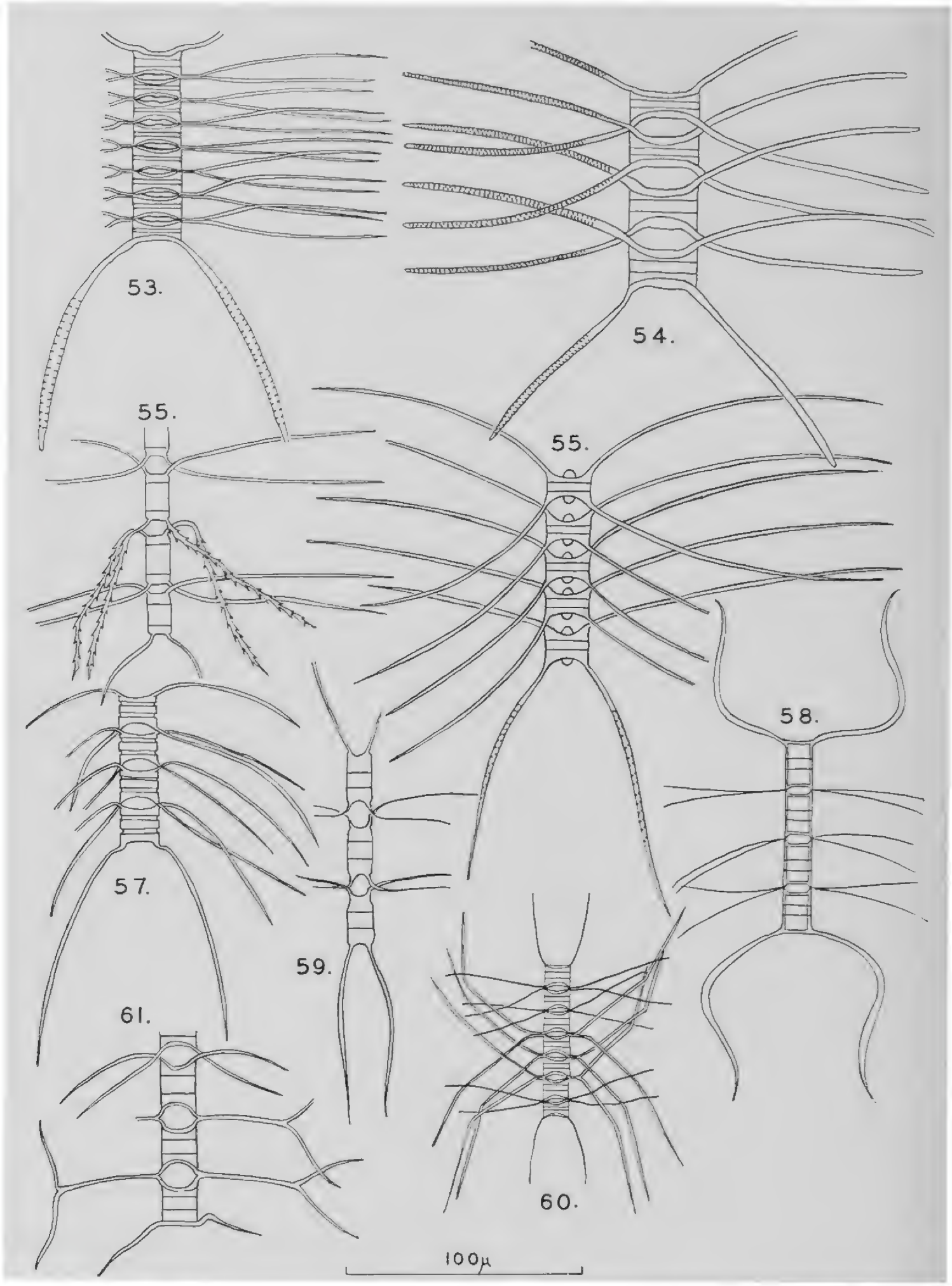


FIG. 53–61. 53. *Chaetoceros decipiens* Cleve, girdle; 54. *Chaetoceros lorenzianum* Grunow, girdle; 55. *Chaetoceros compressum* Lauder, girdle; 56. *Chaetoceros didymum* Ehrenberg, girdle; 57. *Chaetoceros constrictum* Gran, girdle; 58. *Chaetoceros affinis* Lauder, girdle; 59. *Chaetoceros pelagicum* Cleve, girdle; 60. *Chaetoceros diversum* Cleve, girdle; 61. *Chaetoceros messanense* Castracane, girdle.

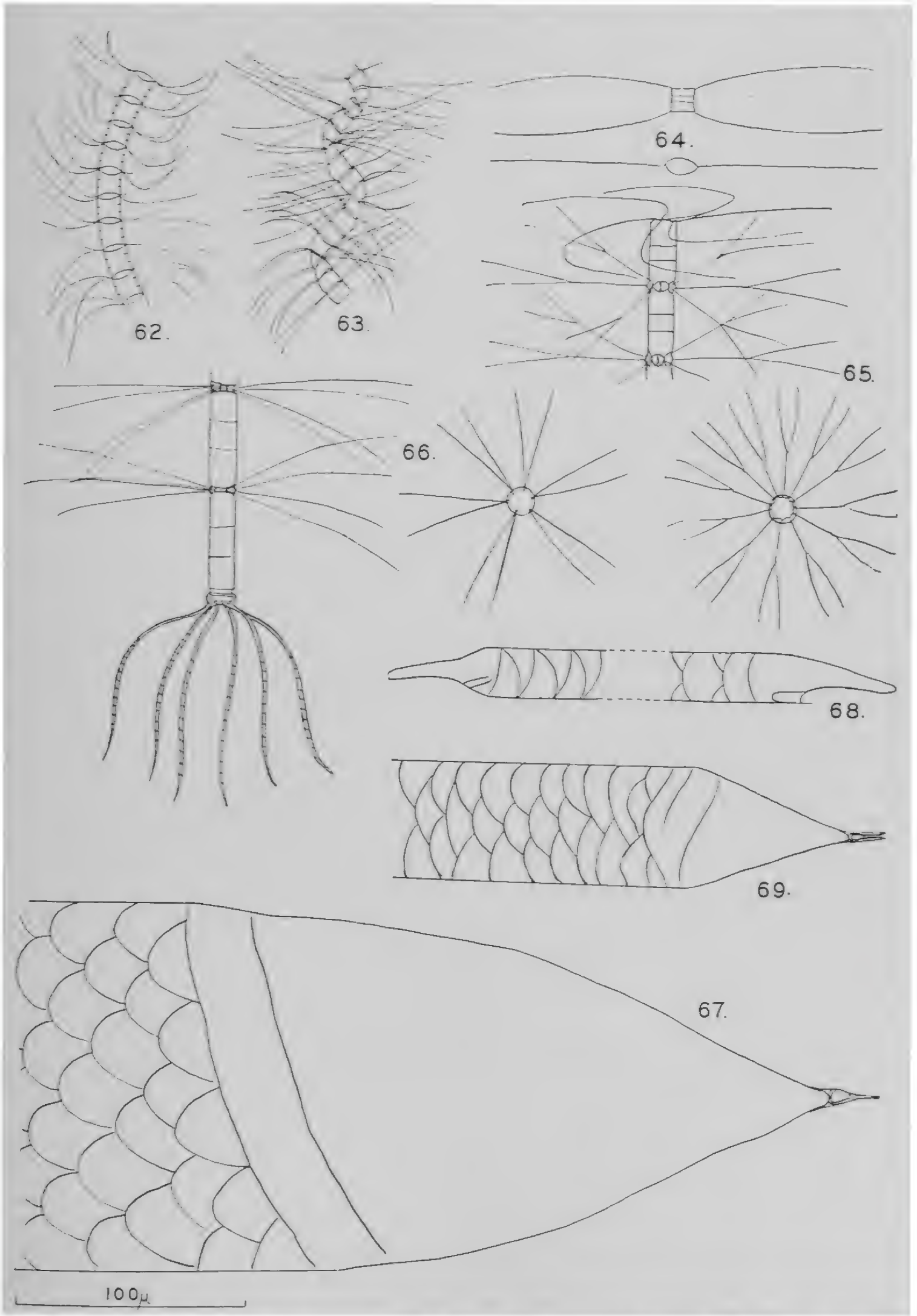


FIG. 62–69. 62. *Chaetoceros currisetum* Cleve, girdle; 63. *Chaetoceros debile* Cleve, girdle: 64. *Chaetoceros gracile* Schütt, a. girdle, b. valve: 65. *Bacteriastrum delicatulum* Cleve, a. girdle, b. valve; 66. *Bacteriastrum elongatum* Cleve. a. girdle. b. valve; 67. *Rhizosolenia acuminata* (Peragallo) Gran, girdle; 68. *Rhizosolenia alata* Brightwell, girdle: 69. *Rhizosolenia bergonii* Peragallo, girdle.

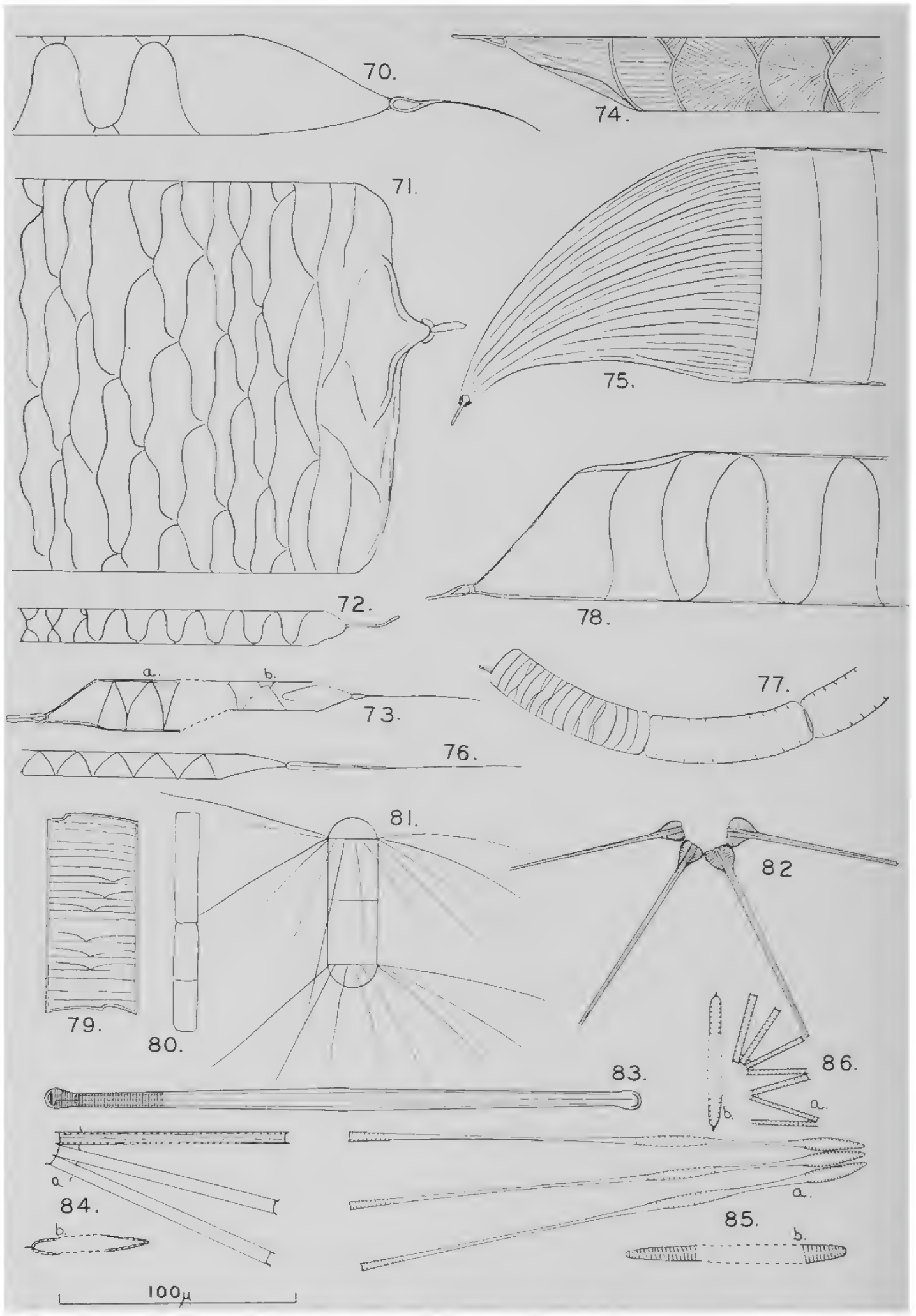
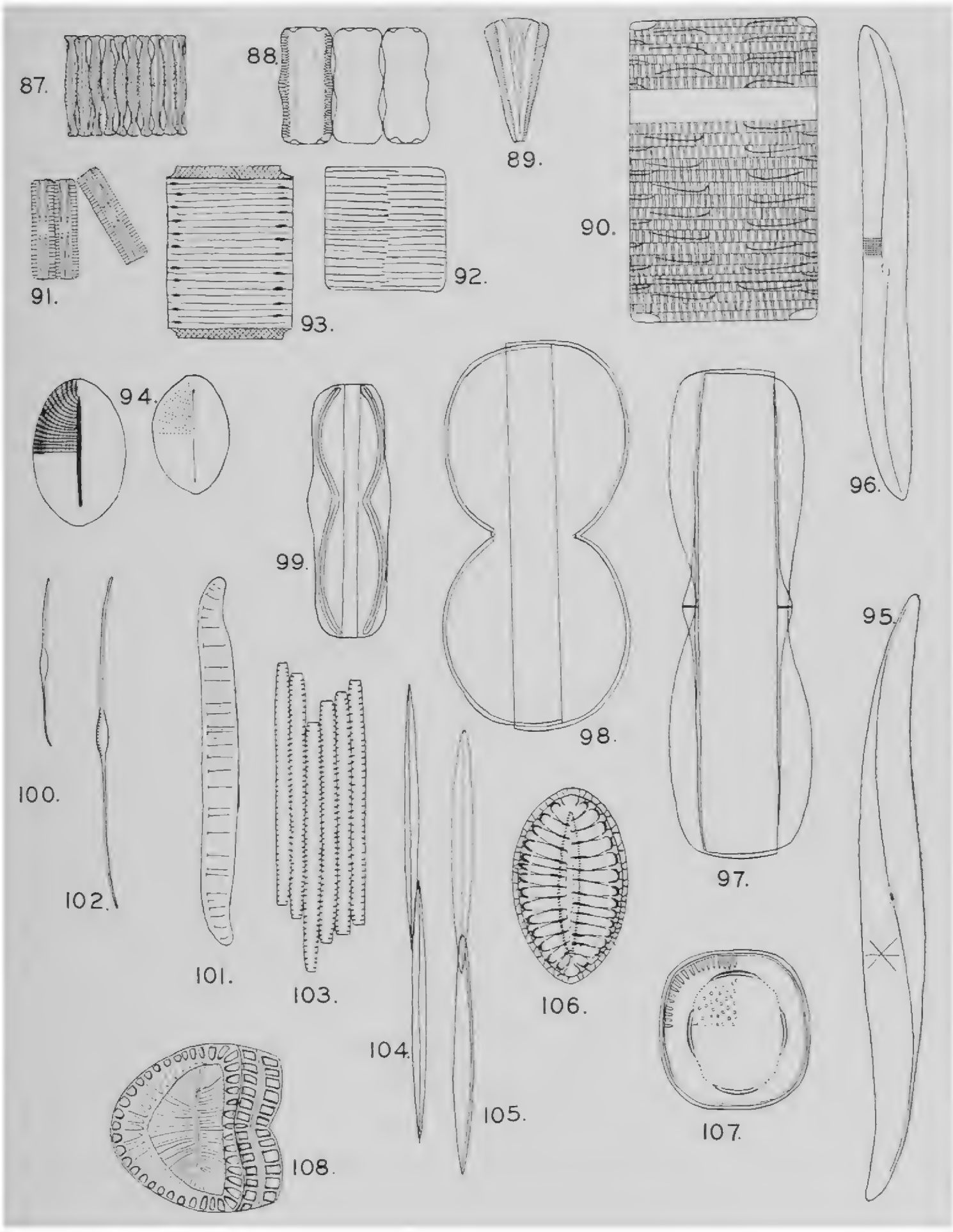


FIG. 70–86. 70. *Rhizosolenia calcar-avis* Schultze, girdle; 71. *Rhizosolenia castracanei* Peragallo, girdle; 72. *Rhizosolenia cylindrus Cleve*, girdle; 73. *Rhizosolenia hebetata* Bailey, a. cold-water form, b. warm-water form; 74. *Rhizosolenia imbricata* Brightwell, girdle; 75. *Rhizosolenia robusta* Norman, girdle; 76. *Rhizosolenia setigera* Brightwell, girdle; 77. *Rhizosolenia stolterfothii* Peragallo, girdle; 78. *Rhizosolenia styliformis* Brightwell, girdle; 79. *Guinardia flaccida* (Castracane) Peragallo, girdle; 80. *Leptocylindrus danicus* Cleve, girdle; 81. *Corethron criophylum* Castracane, girdle; 82. *Asterionella japonica* Gran, girdle; 83. *Synedra fulgens* (Grev.) W. Smith, valve; 84. *Thalassiothrix frauenfeldii* Grunow, a. girdle, b. valve; 85. *Thalassiothrix mediterranea* Pavillard, a. girdle, b. valve; 86. *Thalassionema nitzschioides* Hustedt, a. girdle, b. valve.



F.G. 87–108. 87. *Campylosira cymbelliformis* (A. Schmidt) Grunow, girdle; 88. *Plagiogramma tesselatum* Greville, girdle; 89. *Licmophora abbreviata* Agardh, girdle; 90. *Rhabdonema adriaticum* Kützing, girdle; 91. *Grammatophora marina* (Lyngbye) Kützing, girdle; 92. *Striatella interrupta* (Ehrenberg) Heiberg, girdle; 93. *Striatella unipunctata* (Lyngbye) Agardh, girdle: 94. *Cocconeis scutellum* Ehrenberg, valve; 95. *Pleurosigma decorum* W. Smith, valve; 96. *Gyrosigma balticum* (Ehrenberg) Cleve, valve; 97. *Tropidoneis lepidoptera* (Gregory) Cleve, girdle: 98. *Tropidoneis maxima* (Gregory) Cleve, girdle; 99. *Amphora arenaria* Donkin, girdle; 100. *Nitzschia closterium* (Ehrenberg) W. Smith, girdle: 101. *Nitzschia insignis* Gregory, valve; 102. *Nitzschia longissima* (Brébisson) Ralfs, valve: 103. *Nitzschia paradoxa* (Gmelin) Grunow, girdle; 104. *Nitzschia pungens* var. atlantica Cleve, valve; 105. *Nitzschia seriata* Cleve, a. valve, b. girdle; 106. *Surirella fastuosa* Ehrenberg, valve; 107. *Campylodiscus punctulatus* (Grunow) A. Schmidt, valve; 108.

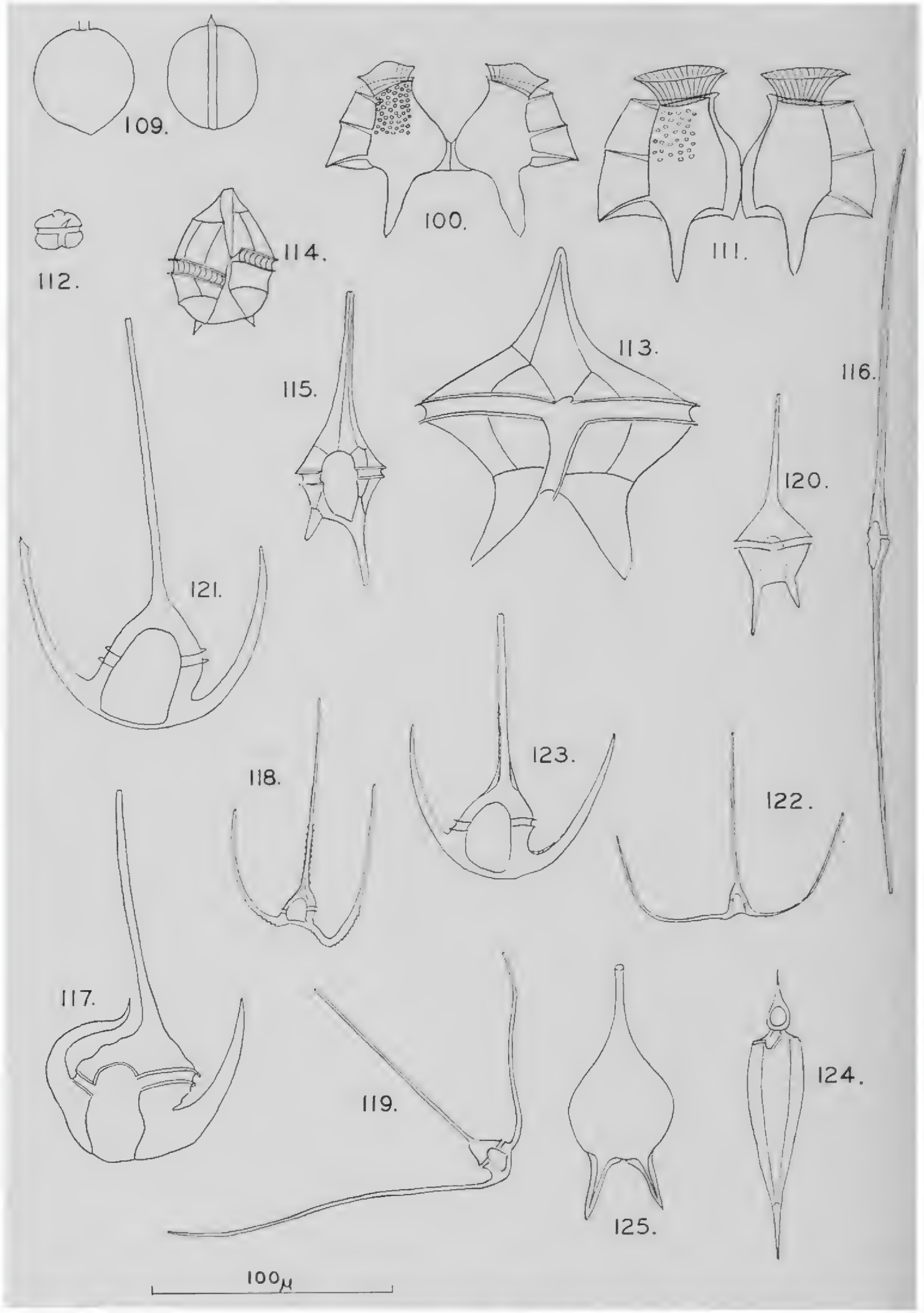


FIG. 109–125. *Campylodiscus samoensis* Grunow, valve; 109. *Exuviella compressa* (Bailey) Ostenfeld; 110. *Dinophysis caudata* Saville-Kent; 111. *Dinophysis tripos* Gourret; 112. *Gymnodinium brevis* Davis; 113. *Peridinium depressum* Bailey; 114. *Goniaulax* sp.; 115. *Ceratium furca* (Ehrenberg) Claparède & Lachmann; 116. *Ceratium fusus* (Ehrenberg) Dujardin; 117. *Ceratium gibberum* Gourret; 118. *Ceratium macroceros* (Ehrenberg) Cleve; 119. *Ceratium massiliense* (Gouret) Jørgensen; 120. *Ceratium pentagonum* Gourret; 121. *Ceratiub pulchellum* Schroeder; 122. *Ceratium trichoceros* (Ehrenberg) Kofoid; 123. *Ceratium tripos* var. *atlanticum* Ostenfeld; 124. *Oxytoxum scolopax* Stein; 125. *Podolampas elegans* Schütt.

A Revision of the Genus Halimeda (Order Siphonales)[1]

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Abstract

A detailed study was made of the structure of the members of the genus *Halimeda* with an examination of their geographic distribution and systematics forming an integral part of this work. Illustrations of habit and histological characteristics, distribution maps, and a key to species are included.

Macroscopic characteristics recognized as important are: appearance, extent of development of the holdfast, morphology of the lowermost one to six segments, and the predominating shapes and sizes of the segments. The microscopic characteristics are: method and extent of development of the cortex, appearance of the inner cortical utricles, average diameter and degree of lateral attachment of the peripheral utricles, and behavior of the medullary filaments at the node. Variations occurring in some of these characteristics during ontogeny are described.

An analysis of the distribution maps shows the genus to be mainly tropical, the boundaries of this and of the subtropical zone being defined by 25°C and 20°C isotheres, respectively, rather than by degrees of latitude. The exceptions are *H. tuna*, which to a limited extent is found also in the subtropics, and *H. cuneata*, which would seem to be mainly restricted to the southern subtropics. Four main types of species distribution occur: pantropical, Indo-Pacific, Pacific, and Atlantic. The five species of the first group, with their disjunct pattern, are of particular interest to the phylogeny of the genus.

In the systematic section the taxonomic characters are evaluated and for each species a description is provided. Species which seem closely related are mainly grouped together within the framework of two categories referred to as the *H. tuna* and *H. incrassata* complexes. Twenty-one species, one variety and one form are recognized, with *H. orientalis* being placed in synonymy under *H. micronesica*, and *H. cylindracea* being established as a species distinct from *H. monile*. Forma *hederacea* of *H. opuntia* is elevated to variety, f. *lata* transferred from *H. gracilis* to *H. lacunalis*, and the other varieties and forms placed in synonymy under the appropriate species. The priority of the species epithet *incrassata* over that of *tridens* is established.

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Introduction

The increase in our knowledge of *Halimeda* during the twentieth century has in a quiet way been dramatic. Since the appearance of the last extensive monograph of the group (Barton, 1901, later Mrs. Gepp) in which seven species and numerous forms were recognized, as many as 12 new species and about the same number of new varieties or forms have been described. For this reason, it is not surprising to find this fine work now restricted in application. In addition, the somewhat changed species concept has made its use more difficult, even in regions from which Barton's specimens originated. A revision of the taxonomy of this genus thus became an important aim of an examination of the morphology and anatomy of the group.

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Historical Treatment

The first substantiated reference to a member of this genus of green algae, is that to a Mediterranean "moss," *Sertolara,* described and illustrated by Imperato in 1599 (Imperato, 1672). This plant, later shown to be *Halimeda tuna,* was included under various names in the writings of succeeding naturalists. Lists of the early synonymy are given by Parkinson (1640) and Bauhin, *et al.* (1650–1651), these writers themselves contributing little towards the establishment of nomenclatorial uniformity by referring to this plant as *Opuntia marina* and *Scutellaria sive Opuntia marina,* respectively. That the history of other species of *Halimeda* does not begin until almost a century later is not surprising, this earliest chapter being Mediterranean, where to the present time *H. tuna* is the only known member of the genus present in the flora.

With the exploration of other lands in the late seventeenth, and the eighteenth centuries, many new plants were collected and described. Important contributions to our knowledge of *Halimeda* during this period are the works of Sloane (1707), physician to the Duke of Albemarle on his trip to the West Indies, and more particularly of Ellis, King's Agent for Dominica and the province of West Florida (1755, 1767), and Ellis and Solander (1786). Plukenet (1691), who examined plants from the Sloane collection, is credited with the earliest description of a second member of this genus, referring to it as both *Corallina latifolia* and *Opuntia marina,* whereas Sloane (1707), in relating the natural history of Jamaica, mentions the plant, *Corallina opuntioides, ramulis densioribus, et foliis magis sinuatis atque corrugatis,* which he equates on the basis of macroscopic criteria, with the *Scutellaria sive Opuntia marina* of Bauhin, *et al.* (1650–1651). Barton (1901), after examining the original specimens on which the descriptions of these three plants were based, placed them in synonymy under *H. opuntia,* whereas a fourth plant, *Lichen marinus rotundifolius* (Buddle MS in Herb. Sloane, *in* Barton, 1901), was identified as *H. incrassata.*

Ellis (1786), in a book completed posthumously by Solander, includes descriptions

and excellent illustrations of five species of *Halimeda* as *Corallina incrassata, C. opuntia, C. monile, C. tridens,* and *C. tuna,* the first two having been referred to in an earlier work (1755) as the *Articulated Corallines of Jamaica.* The figures given for some of these (1755, Plate 25, Figures A, A_1, B, B_1; 1767, Plate 17, Figures 22–27; 1786, Plate 20, Figures d_{1-3}, D_{1-6}) are of particular interest, microscopic details being included for the first time.

The natural history of the corallines held particular fascination for Ellis. The group at that period included members of the animal phylum Coelenterata in addition to representatives of the algal orders Cryptonemiales and Siphonales, the genus *Halimeda* belonging to the latter. During the course of his investigation, he observed polyps within certain of these organisms, and consequently relegated the entire assemblage to the animal kingdom. Such treatment was subsequently upheld by Linnaeus in his *Systema Naturae* (1758, 1766–1767). The latter felt that the presence of calcareous material indicated an animal origin and classified *Corallina opuntia,* representing both *H. opuntia* and *H. tuna,* among the Zoophyta or animal-plants, a group comparable to Ellis' corallines as described above. Other naturalists, including Pallas (1766), objected to an animal classification of the Linnaean genus *Corallina,* since the actual polyps had not been observed in members of this taxon. However, a year later, in a letter to Linnaeus (1767), Ellis argued strongly in favor of the zoological affinities of this group. His points were based partly on the morphological similarities between the corallines and certain genera in which polyps had actually been observed. When microscopes were improved he felt the polyps of the corallines would be readily seen. Other arguments dealt with their chemistry, and included the fact that when burned, members of this group produced "an offensive smell like that of burnt bones or hair," rather than the odor of scorched vegetables. Ellis' arguments were sufficiently convincing that the corallines were retained in the animal kingdom by many succeeding taxonomists, including Lamarck and Lamouroux although these workers substituted the term "polypier" for "zoophyte." Nevertheless, an important advance in the taxonomy of this group was made by Lamouroux who, considering the corallines a composite, delimited several genera including *Halimedea* (1812), or *Halimeda* (*orth. mut.,* 1816). At the 1956 Botanical Congress this name was conserved over that of *Sertolaria* which had been proposed by Boehmer (in Ludwig, 1760), the type specimen for the latter being Imperato's plant *Sertolara.* Assigned to this new taxon were the five species of *Corallina* described by Ellis, and *C. discoidea* Esper. This last species, presumably based on a Mediterranean plant, was later placed in synonymy under *H. tuna* by Hammer (1830) in his continuation of Esper's work.

The succeeding period saw the removal of several genera including *Halimeda* from the animal kingdom by various researchers including Link (1834), Chauvin (1842), and Decaisne (1842), and the description of many new species, increasing the total to 27. These were collected by naturalists accompanying various exploratory expeditions, and are found in the works of Decaisne (1841, 1842), Krauss (1846), Kützing (1857–1858), Zanardini (1851, 1858), Piccone (1879), Hauck (1886), J. Agardh (1887) and Askenasy (1888).

Although Ellis, as early as 1755, included figures showing details of microscopic organization, few anatomical studies were attempted. The delimitation of new species up to the time of Askenasy (1888) was based almost entirely on macroscopic characteristics, with Kützing (1857–1858) remarking on the general uniformity of the internal

organization. Agardh (1887) in his taxonomic treatise indicated the possibility of nodal fusion, but the first detailed histological study was that of Askenasy who described and figured the method of fusion occurring among the nodal medullary filaments in *H. incrassata* (including *H. cuneata* Kützing which was misnamed), and suggested that the size and shape of the peripheral utricles were characteristic for most species.

The ground work was thus laid for a monographic work, the need for which was realized by Barton (later Mrs. Gepp) while working on the Halimedae collected by the Royal Society coral-boring expedition at Funafuti in the Ellice Islands. In her report (1900), she pointed out that *H. cuneata* Hering and *H. cuneata* Kützing were different plants, and that the latter would require a new name in a revision of the genus. Such a study she herself undertook shortly afterwards (1901) in conjunction with an examination of material collected by the Siboga Expedition. For the first time the numerous species were examined by one person, these being compared with type specimens whenever possible. A fairly detailed microscopic examination resulted in the recognition of two types of nodal medullary filament behavior in addition to that described by Askenasy for *H. incrassata*, the one being typified by *H. opuntia*, the other by *H. gracilis* and *H. tuna*. On the bases of a rigid adherence to the taxonomic importance of this characteristic, and of the recognition of many intermediates, only seven species were retained. The others were reduced to forms or placed in synonymy.

This approach succeeded in indicating relationships between some of the earlier described species, and established a certain degree of order, most notably in the *H. opuntia* group. Her treatment, however, was somewhat inconsistent, the taxon f. *ovata*, for example, being classified as a subdivision of *H. incrassata* although the behavior of the nodal medullary filaments in the two is quite different. In addition, Barton's species concepts, based largely on the single characteristic of nodal structure, generally seem to be more of the nature of subsections or series, and tend to submerge the individuality of many species. Thus, only a few years later, *H. discoidea* and *H. monile*, two entities not accepted as distinct at the species level by Barton, were reestablished by Howe (1907), who pointed out the usefulness of two other taxonomic characters in particular: the appearance of the inner cortical utricles, and the average diameters of the peripheral utricles measured in surface view. Working on representatives of this genus in the eastern North American flora, Howe also described and figured four new species, including *H. simulans*. The rank he assigned to *H. monile* and *H. simulans*, as well as the use of the epithet *tridens* rather than *incrassata* for the taxon resulting from the combination of these two species, were subsequently criticized by Børgesen (1911, 1913). The result was a disconcerting lack of uniformity, with American workers in general adopting Howe's system of regarding *H. monile* and *H. simulans* as distinct species, and using the epithet *tridens*. Europeans and Asiatics have usually followed Børgesen in his usage of the epithet *incrassata*, and have consequently considered *H. monile* and *H. simulans* as varieties or forms of *H. incrassata*.

The next phase in the history of this group was centered on collections from the western Pacific, with Yamada in 1941 describing a new species, *H. micronesica*, from the Caroline Islands. This addition was of particular interest since it represented a category of nodal medullary filament behavior unlike those recognized by Askenasy and Barton. A second species with this type of nodal anatomy, *H. fragilis*, was described by Taylor (1950) from his collections made in the Marshall Islands during 1946 in conjunction with the detailed scientific study of these atolls by the armed services. As a result of

Taylor's work, a total of six new species and two new forms of *Halimeda* were described.

This present revision is world-wide in scope, part of its limitations being the general lack or unavailability of specimens from certain areas. The concept of species embodied is fairly broad in order to include within the described limits what has been regarded as the variation occasioned by environment.

Morphology, Anatomy and Reproduction

Methods

Herbarium specimens have been an important source of information, the data obtained through an examination of these being compared with those from fluid-preserved plants, some of the latter material having been collected by the author in Florida.

Histological preparations for studying simultaneously the anatomy of the segment or internode and the node were made by removing a narrow rectangular strip cut so as to extend from the middle of the internode of one segment where the most typical development of the cortical layers occurs, through one of the adjoining nodes. Since only a portion of the node is removed, the segments involved remain attached. Segments in all stages of development were sectioned for anatomical studies, but only mature ones were selected for taxonomic considerations.

Thin sagittal sections were cut from this rectangular sample, a glass microscope slide, held somewhat obliquely with one of the narrow edges touching the material, serving to hold the tissue firmly in place and functioning as a guiding edge for the cutting. The sections were floated in water on a slide, decalcified with approximately 25 per cent hydrochloric acid, and mounted in glycerine solution.

Such longitudinal sections were supplemented with transverse sections of the internode and node, and with thin sections removed from the surface. The last were used to measure the diameters of the peripheral utricles.

The separate study of nodal anatomy was by dissection, using either the longitudinal sections described above, or unsectioned nodal material. Insect mounting pins or fine needles were useful in teasing apart adhering filaments and in the elucidation of the more difficult conditions. These preparations were supplemented with transverse sections through the node which often more readily indicate the pores between adjacent medullary filaments, if fusion is of the *H. incrassata* type. A preliminary insight into the type of nodal structure present can sometimes be gained by noting whether the filaments hang firmly together after declacification or tend to separate. The behavior should always be confirmed by dissection, however, since in dried specimens particularly the filaments may adhere.

Habit and External Form

The habit (Plates 1–4) may be erect, decumbent or prostrate, and is quite distinctive for certain species as exemplified in the rather flaccid, straggling plants of *H. gracilis* (Plate 2, Figure 4) and *H. lacrimosa* (Plate 2, Figure 2), or in the erect plants of many species of the *H. incrassata* complex. The general appearance is at times somewhat modified as in certain specimens of *H. lacunalis* (Plate 1, Figure 1) and *H. tuna*, by the occurrence on the same individual of segments apparently produced during two or three

separate growing periods, or by the regeneration of a new upright system from the basal segments (Plate 4, Figure 2), this seeming to be of fairly common occurrence among members of the *H. incrassata* complex. In *H. opuntia* (Plate 2, Figure 7), particularly in many of the Pacific specimens, both axial and lateral growth systems are frequently present on the same plant, these being more completely described in the taxonomic treatment of this species. A somewhat similar pattern of growth may be found in plants of *H. micronesica.*

A single holdfast region is usually present. This is generally one cm long or less in *H. fragilis, H. micronesica,* and members of the *H. tuna* complex, but is nearly always extensively developed in species of the *H. incrassata* group, extending to 13 cm in length in *H. stuposa.* In such types, the rhizoids interlace with particles of the substratum to form a compact, massive structure which remains intact when the plants are collected. In contrast, several areas of attachment occur in *H. opuntia,* the rhizoids arising from the nodes. In addition, prostrate branches in this species and in *H. micronesica* may terminate in rope-like extensions consisting of intertwined rhizoidal filaments to a length of approximately six cm (Plate 3, Figure 1). Microscopically, the holdfast generally consists of thick-walled filaments which branch dichotomously or laterally. The resultant rami, which are often of smaller diameter and with relatively thinner walls, in turn fork dichotomously (Plate 8, Figure 1), the numerous small branches sometimes twining around the main filaments to produce the rope-like or fibrous appearance mentioned above. Inward projections from the rhizoid walls, that do not necessarily occur at the sites of branching as is usually the case for medullary filaments of the frond, may partially, or at times perhaps completely, obstruct the lumen.

The photosynthetic portion of the plant is composed of disjunct, calcified, variously-shaped internodes or segments, the term "joint" also, at times, being used in the literature. These are connected by narrow, uncalcified, flexible nodal regions, the species *H. cuneata* (Plate 1, Figure 6) representing a special case, with a small cushion segment, or stalk region, or both, frequently interposed between the node and internode. This modification is discussed in the systematic treatment of this taxon. The basal segments are often golden or copper-colored, and are generally thicker and more strongly calcified than the others. They may also be modified in shape. In members of the *H. incrassata* complex two pattern types are frequently noted. Several of the lowermost segments may remain unbranched producing a caulescent aspect, or adjacent basal segments may consolidate laterally forming a rather massive fan-shaped structure (Plate 4, Figure 1). The most extreme modification of basal segments, however, is found in *H. micronesica* (Plate 3, Figure 1) where the lowermost segment is usually several times larger than the other segments on the plant, and is very irregular in outline.

The remainder of the segments are plane or ribbed, spherical to cylindrical, tear-shaped, compressed-cylindrical, or cuneate to reniform in shape, with the upper margin of broad flattened segments entire, undulating or lobed. Several shapes may occur in a single species, but frequently one or more will predominate. Thus, *H. lacrimosa* is characterized by spherical and tear-shaped segments although cylindrical ones are also present, whereas in members of the *H. incrassata* complex subcuneate segments with lobed outer margins, and cylindrical ones commonly occur. In size, the range extends from the small mature segments of *H. lacrimosa,* to those of *H. gigas,* these to 25 mm in length and 42 mm in breadth with the width generally exceeding the length. The thickness of the segment varies with the number and height of the cortical layers, but usually

decreases from base to apex within the same specimen. Their color is influenced by the degree of calcification, proceeding from green to white with an increase in calcium carbonate. Very young segments which are completely uncalcified are thus dark green, whereas well-developed basal segments are often gold-colored as a result of the increased calcification and the frequent occurrence of yellow pigments within the filaments and their walls. However, the amount of calcification varies not only within the same specimen but also to a certain extent with ecological distribution and with the species. Thus, deep-water specimens of *H. tuna* and *H. discoidea* are generally less calcified than are shallow-water members of these same species. Specimens of *H. cuneata* and *H. lacunalis* are often rather lightly calcified, whereas those of *H. fragilis, H. gracilis, H. lacrimosa* and *H. bikinensis* are usually heavily calcified, their brittle segments requiring special pretreatment with acid before satisfactory sections can be cut. The details of calcium carbonate deposition which begins along the lateral walls of the peripheral utricles directly below the region of their adhesion, have been discussed by Askenasy (1888), his observations having been translated by Barton (1901).

Internodal Anatomy and Ontogeny

The relatively complex organization of an internode is the result of the ramification and interweaving of coenocytic filaments, the walls of which are composed mainly of callose impregnated with pectic compounds (Mirande, 1913). The genus resembles *Caulerpa* in this respect, but differs from other members of the Siphonales, such as *Bryopsis, Codium* and *Derbesia*, in which cellulose is present in addition to the above materials. The walls for the most part are relatively thin, except for the occurrence of annular constrictions at the bases of the branches or of the utricles which at times are very pronounced and may possibly even obstruct the lumen. Such constrictions may represent a mechanism for the restriction of protoplasm in the absence of cross walls, a second possible method being the accumulation of mucilaginous material within the filaments in such a way as to almost or entirely block them. The latter condition has been reported for other members of the Siphonales as a response after wounding (Mirande, 1913).

With the growth and development of these filaments, two main regions of an internode are delimited: an inner multiaxial core of lengthwise-extending medullary filaments which generally branch trichotomously, and a surrounding cortex of two or more layers or zones of utricles. These utricles develop from the lateral branches of the central filaments and may be delimited in two ways, the more common of which is by the occurrence of constrictions at the sites of branching, followed by the enlargement of the intervening regions. The second type involves a succession of dichotomies unaccompanied by swellings, constrictions in these species being rather poorly developed or absent (Plate 6, for both types). The second type is found in *H. bikinensis, H. fragilis, H. micronesica, H. opuntia,* and to a lesser extent in *H. gracilis* and *H. lacrimosa,* whereas the first occurs in the remaining species, with the most conspicuous development in *H. discoidea.*

Additional variation within the cortex occurs mainly with respect to the number of layers or zones, the size and shape of the utricles of the cortex, the degree of lateral attachment of the peripheral utricles, the number of peripheral utricles supported by each secondary one (i.e. the second from the periphery), and the amount of calcification. The number of layers comprising the cortex may be distinctive of the species, ranging

from two to five, rarely six, with two zones generally present in *H. discoidea, H. gigas,* and *H. macrophysa,* and five layers in *H. opuntia* and some species of the *H. incrassata* complex. In addition, a limited amount of variation may occur within the same internode. Thus, in *H. discoidea* (Plate 6, Figure 11), an additional zone may occasionally be present although not with any apparent uniformity, whereas in *H. lacunalis* two layers rather than the more usual three may occur. The extent of development of the cortex also varies somewhat with position in the internode, and with its age. Thus, the inner cortical layers are frequently reduced or absent in the vicinity of the node, the peripheral utricles being supported directly by the main branches of the medullary filaments (Plate 7, Figures 1, 8, 13). In young segments there may be fewer cortical layers (Plate 6, Figures 21–22), whereas an increase over the more usual number may occur in thickened and older basal internodes (Plate 6, Figure 24).

The shapes and diameters of the inner cortical utricles are very distinctive for certain species, the most notable being the inflated secondary utricles of *H. discoidea* (Plate 6, Figure 11), which average 125 microns in breadth with adjacent ones frequently contiguous. In *H. taenicola* (Plate 6, Figure 14), the tertiary utricles are considerably expanded, whereas in the species with utricles formed by successive dichotomies in the lateral branches of the medullary filaments, the diameters are generally those of the filaments. In the latter case, however, the ends of the secondary utricles may at times become somewhat expanded, particularly just prior to the development of a dichotomy. In *H. lacrimosa* (Plate 6, Figure 12), and to a slight extent in *H. gracilis* (Plate 6, Figure 9), the secondary utricles are regularly swollen, and appear capitate or clavate; in *H. tuna* they are frequently obpyramidal; in members of the *H. incrassata* group the secondary and tertiary utricles are generally globular or subglobular. The inner cortex is least well developed in *H. macrophysa* (Plate 6, Figure 8). The lengths of the utricles of the inner cortex are less constant than the diameters, this variable being influenced by the numbers of utricle layers and consequently, to a certain extent, by the age of the segment (Plate 6, Figures 21–24).

The peripheral utricles are generally well delimited by basal constrictions and usually appear cylindrical to conical in section, the upper surface being extended into an indurated spine in *H. scabra* (Plate 6, Figure 4). In *H. stuposa* (Plate 5, Figure 25) and occasionally in other species, their outer and lateral walls may be somewhat thickened throughout the entire segment, this in other types generally being restricted to the vicinity of the node or to mature basal segments (Plate 5, Figure 23). Adjacent utricles in *H. cuneata, H. discoidea, H. gigas, H. taenicola,* and *H. tuna* may fuse laterally in twos, threes, or rarely fours for as much as one-half their length (Plate 6, Figures 5, 11; see also Plate 5, Figures 1, 9, 11, 12). However, in most species the utricles merely adhere laterally to form a continuous surface, the extent of adhesion varying considerably. In *H. cuneata* and *H. discoidea* this may be for approximately one-half their length or about 40 microns, in *H. opuntia* for an average of 4 microns, whereas in *H. lacrimosa* and *H. gracilis* this region is restricted to a thin platform-like extension of the outer surface of the utricle, these detaching fairly readily with pressure after decalcification. In *H. macrophysa* (Plate 5, Figure 16), *H. fragilis* (Plate 5, Figure 10) and usually in *H. favulosa* (Plate 5, Figure 24), *H. macroloba* (Plate 5, Figure 19), and *H. micronesica* (Plate 5, Figure 13), the utricles are laterally free, being separated at least to a certain extent by calcareous partitions. These are particularly well-developed in *H. macrophysa.* This degree of lateral attachment varies somewhat with the age of

the segment, the peripheral utricles in immature apical segments of *H. bikinensis* (Plate 5, Figure 18), *H. micronesica* (Plate 5, Figure 14), *H. macroloba* (Plate 5, Figure 20), and occasionally other species, often remaining relatively firmly attached after decalcification, although tending to separate in mature segments. In other species, particularly members of the *H. incrassata* complex, the utricles, although generally adhering in young and mature segments, may separate somewhat readily in well-developed basal ones where their walls are frequently thickened as has been described.

The surface appearance (Plate 5) of the peripheral utricles is largely determined by their juxtaposition, firmly attached ones appearing more or less regularly polygonal (usually hexagonal) as a result of the pressures they exert on each other. Those of *H. gracilis* and *H. lacrimosa* which adhere by a platformlike extension, may at first appear rounded, but with critical focusing faint hexagonal lines often become visible. The illusion of roundness is the result in part of the slightly convex outer face of the utricles. In species such as *H. macrophysa* in which the utricles are separated by calcareous partitions, they appear round, and in general do not maintain an erect orientation unless the decalcification has been incomplete. The average surface diameter of the peripheral utricles is a fairly constant species characteristic, the smallest utricles occurring in *H. opuntia*, the largest in *H. favulosa*. Their lengths, however, are more variable, generally increasing in basal segments (Plate 6, Figures 23–24). Usually two or four are supported by each secondary utricle. However, in *H. favulosa* at times only one occurs on each secondary utricle, in *H. bikinensis* and *H. gracilis* up to eight may frequently be so supported, with as many as 14 in *H. discoidea*, and 18 in *H. lacrimosa*. Numbers intermediate between two and eight may be found in stages preceding the delimitation of additional secondary utricles in species in which two or four are the more usual numbers.

In the formation of new joints, the initial step involves the extension of the medullary filaments past the node (Plate 6, Figures 21–22). Somewhat more advanced stages are figured by Askenasy (1888) for *H. discoidea* (miscalled *H. macroloba*) and *H. opuntia*. During subsequent development these filaments elongate and branch trichotomously to produce the cortex, the methods of delimitation of the inner cortical utricles having been described earlier in this section. These utricles in turn bud off peripheral ones to form a closely packed surface layer. The pectic material in their walls probably aids lateral adhesion, the degree of which, as previously discussed, often somewhat exceeds that found in mature segments. Although at this stage the filaments are devoid of chloroplasts, the main structure of the joint, a medulla and cortex with an outer layer of utricles which generally adhere, is complete. Subsequent development involves the deposition of calcium carbonate and generally a greater elaboration of the inner layers, this depending on the species.

Nodal Anatomy

The species of *Halimeda* can be segregated into three main categories on the basis of the behavior of the medullary filaments at the node (Taylor, 1950), the filament walls in this region generally being golden in color and thickened to as much as 15 microns. In the first of these groups, as represented by *H. fragilis* (Plate 7, Figure 1) and *H. micronesica*, the filaments continue unchanged throughout the node, although adjacent ones, particularly of the latter species, may adhere slightly in the nodal region.

The second main type (Plate 7, Figures 2–10) occurs in the *H. tuna* complex, the

filaments most commonly fusing in twos or threes, then either separating almost immediately into twos or threes (Plate 7, Figure 3), or continuing as single filaments for several times the length of fusion before dividing trichotomously (Plate 7, Figure 2). These two methods of fusion in small units have frequently been referred to as "incomplete" and "complete" fusion, respectively. These two terms are rather misleading since they may be interpreted as indicating that only a few, or all of the filaments are involved. Hence, the terms "short" and "extended" are suggested for designating the length of fusion, with *H. opuntia* being an example of the former. The second type is found in *H. gracilis, H. lacunalis, H. macrophysa,* and *H. taenicola,* whereas both are present in *H. bikinensis, H. cuneata, H. discoidea, H. gigas, H. lacrimosa, H. scabra, H. tuna,* and possibly *H. taenicola,* the short form at times seeming to be more common towards the periphery of the node. In *H. lacrimosa* (Plate 7, Figures 5–6), and on occasion in the Mediterranean *H. tuna,* short and extended fusion, rather than existing side-by-side are combined in the same unit, with two filaments arising immediately after a fusion of three or four. In rare cases in species of this second main group a filament may remain unfused, or short fusion in fours may occur. Below the node the medullary filaments have usually branched ditrichotomously. Many of the smaller rami from this division support peripheral utricles (Plate 7, Figures 1, 8, 13), whereas the main filaments and some of the branches unite in such a fashion that the resulting fused units are frequently greatly entangled (Plate 7, Figures 7, 10). These units at times may adhere laterally, and often for considerable distances as in *H. lacunalis* (Plate 7, Figure 8), or for shorter lengths as in *H. taenicola.* In the Caribbean *H. tuna,* extended fusion seems to be the rule. Lateral attachment may occur in other species but it is generally extremely short.

The third main category of nodal behavior is exemplified by the *H. incrassata* complex (Plate 7, Figures 11–13), and can perhaps be regarded as a further development of the short fusion defined above, with *all* of the filaments, occasionally a peripheral one excepted, uniting for a short distance into a single unit at the node. The walls between the filaments in this region do not disintegrate completely, but become perforated, the resultant thick-walled pores being visible in longitudinal and transverse sections. The pore diameter varies to a certain extent both inter- and intra-specifically but without apparent regularity, and the connecting regions between filaments sometimes become slightly prolonged so that the main filaments appear to be united by short tubular processes. This is particularly so when the pores are small, and since such narrow processes are fairly readily severed, the mode of fusion may then possibly be mistaken for short lateral adhesion. This third main category of fusion is least well-developed in *H. monile* (Plate 7, Figure 12). In this species, the medullary filaments are rather strongly united in twos, threes or larger numbers, these groups in turn being connected into a single unit by narrow tubular processes.

Reproduction

The reproductive history of this genus is not well known. Fertile individuals are rarely collected, and have been reported for less than half of the species, including *H.? cuneata* (Chihara, 1956), *H. discoidea* (Egerod, 1952), *H. gracilis* (Gepp, 1904), *H. macroloba* (Zanardini, 1876; Schmitz, 1880; Weber-van Bosse, 1926; Kanda, 1940), *H. monile* (Howe, 1915), *H. scabra* (Howe, 1905a; Taylor, 1924, 1925, 1928), *H. simulans* (Howe, 1915; Taylor, 1928), *H. incrassata* (Howe, 1907; Taylor, 1928; both as *H. tridens*), *H. tuna* (Derbès and Solier, 1956; Bompard, 1867; Schmitz,

1880; Gepp, 1904; Howe, 1907; Nasr, 1947), and *H. tuna* f. *platydisca* (Schmitz, 1880; Feldmann, 1951). Until recently the nature of the biflagellated zöoids which had been observed by Derbès and Solier (1856), and Schmitz (1880) was unknown, and they were referred to in the literature as both zöospores and gametes. Nasr (1947) and Chihara (1956) have reported fusion between these zöoids, and Chihara (1956) and Feldmann (1951) described them as anisogamous, the macrogamete with brownish-green plastids and a posterior eyespot, the microgamete with green plastids and lacking a stigma. These are contained in gametangia which appear in grape-like clusters, arranged alternately or spirally, and in the specimens studied indeterminately, on stalks which are simple or one to two times forked (Plate 8, Figures 2–13). Feldmann (1951) reported the discharge of the densely-packed contents of the segment filaments into the gametangia of *H. tuna* f. *platydisca* leaving the tubes almost empty. The occurrence of plugs or septa in the gametophores was noted by Howe for *H. scabra* (1905a) and for certain Caribbean specimens of *H. tuna* (1907), although in this second species their presence was apparently an irregular feature. By analogy to other members of the Siphonales such plugs might perhaps be expected, but they have not been confirmed by other workers, and were not observed in the material examined.

The gametophores occur along the margin or on the surface of the segment, and arise in three ways: (1) as continuations of the main medullary filaments subsequent to their fusion, which seems similar to the mode of fusion occurring at the nodes, at least in the species for which this is known (Plate 8, Figures 5, 8, 11, 13), (2) as lateral outgrowths without fusion from medullary filaments (Plate 8, Figures 9–10), and (3) as extensions from peripheral or secondary utricles (Plate 8, Figures 2, 6, 7, 12), (Howe, 1907). Howe (1905a), in comparing the fruiting branches of *H. scabra* with those of *H. tuna* as described by Gepp (1904), concluded that there were no significant differences between the two, a conclusion which would seem to hold true for the other species examined in this study. Variation occurred in the degree and site of branching of the gametophores, but since they vary considerably within the same species, such characteristics are of little value taxonomically. The size of the mature gametangia and the method in which the gametophores arise from the segment in the various species may prove significant when sufficient material becomes available for a comparative study.

Geographical Distribution and Ecology

The establishment of climatic zones corresponding to torrid, temperate and frigid is attributed to Aristotle, and followed upon the acceptance of the earth's spherical nature by the early Greek scholars. As the basis for a classification of vegetation, this scheme has various limitations which for algae have been essentially overcome in the system proposed by Setchell (1915) which consists of nine temperature zones rather than the usual three or five, their boundaries, except for the outermost, being established by 5° C isotheres. Thus, in the northern hemisphere, the Upper Boreal includes waters with temperatures up to 10° C, the Lower Boreal 10–15° C, the North Temperate 15–20° C, the North Subtropical 20–25° C, and the Tropical 25° C and higher, this latter zone being common to both hemispheres. In the southern hemisphere similar ranges are covered by the Upper Austral, Lower Austral, South Temperate and South Subtropical. Classified according to this system, the species of *Halimeda*, with the exception of *H. cuneata*, are tropical. This one species is almost entirely subtropical, whereas *H. tuna* appears capable of existence in both zones.

The distribution for the individual species is shown in Plates 9–12 to which the tropical and subtropical isotheres have been added, using as reference Sverdrup *et al.* (1942). The points plotted are based on data obtained mainly from the various herbarium collections examined. This information has been extended for one species, *H. macrophysa*, a plant which cannot readily be confused with any other, by the use of the literature references which are listed under its taxonomic treatment. Such a restriction of data was felt necessary since the definition of the various species has changed considerably during the taxonomic history of the genus, with the result that many of the early checklists cannot be used without verifying the identification of the specimens. In the ensuing discussion of this distribution the literature cited has in some cases been restricted to the more recent or extensive publications.

An analysis of these plates shows the following categories of distribution: (1) pantropical (excluding the Mediterranean), five species; (2) Indo-Pacific, seven species; (3) western Atlantic, four species; (4) Mediterranean, one species; (5) western Atlantic-Pacific, one species; and (6) Pacific, four species, with the last two groups probably resulting from incomplete information. The species representing the fifth category, *H. simulans*, has a fairly extensive distribution among the Caribbean Islands, and occurs also in the vicinity of Recife, Brazil. It has been collected to a limited extent in both hemispheres of the Pacific, but as yet is unknown for the Indian Ocean. The members of the sixth category are *H. gigas*, represented by a single collection obtained at 46 meters depth, *H. lacunalis*, *H. taenicola*, and *H. macrophysa*. The first three of these are known only for the North Atlantic, whereas the last species has been collected in both hemispheres.

The species with pantropical distribution, *H. discoidea*, *H. gracilis*, *H. opuntia*, *H. incrassata*, and *H. tuna* are of particular interest since they provide some insight into the phylogeny of the genus. Of the various attempts to explain such disjunct distribution between the Indo-Pacific and Atlantic Oceans, Murray's theory (1889) involving a migration of tropical floras around the Cape of Good Hope during warmer epochs has been superseded by that of Svedelius (1924), who pointed out that prior to the formation of the present Isthmus of Panama in Miocene times, the floras of the Atlantic and Pacific had been connected several times in the Central American region. On the basis of this theory the pantropical species, representing two out of the three types of nodal behavior, must have been well developed at least by the early Miocene.

One-third of the species, *H. bikinensis*, *H. cuneata*, *H. cylindracea*, *H. fragilis*, *H. macroloba*, *H. micronesica*, and *H. stuposa*, have an Indo-Pacific distribution, that of *H. cuneata* being the most noteworthy. This species appears to be restricted almost entirely to the southern subtropics, extending along the eastern shores of Cape Province, Africa, to the tip (Krauss, 1846; Barton, 1893; Isaac, 1953), and along the southwestern shores of Australia, whereas in the southern Pacific it occurs at Lord Howe Island. Although the subtropical nature of this species was recognized by Barton (1901), its distribution has been greatly extended by specimens of *H. discoidea* frequently being misidentified as *H. cuneata* (Gilbert, 1947; Papenfuss and Egerod, 1957). Indeed, many of the specimens observed during the course of this study, most particularly those from northeastern Australia and Japan proved to be other species, and most commonly *H. discoidea*.

Within the tropical Indian Ocean a diversified flora of *Halimeda* seems to exist, being best known for eastern Africa, Ceylon, and many of the western reef islands and

atolls including the Seychelles and Mascarene Islands (Schröder, 1912; Jadin, 1935; Børgesen, 1936, 1940, 1946). Only a few of the species, however, including *H. cylindracea, H. discoidea, H. macroloba, H. opuntia,* and possibly *H. tuna,* are known to extend into the Red Sea. This region also represents the type locality for *H. nervata* and *H. papyracea* (Decaisne, 1841; Zanardini, 1858; Piccone, 1884; Nasr, 1939, 1947). The same species, but including *H. tuna,* are found in the Gulf of Aden. Although there are several short lists of algae in existence for the Persian Gulf, this genus has not yet been reported.

Within the Pacific, this genus is much better represented in the western than in the eastern half. The flora of the Marshall Islands can perhaps be considered as typical of the region possessing at least 13 out of the 17 species of *Halimeda* known for the Pacific: *H. bikinensis, H. cylindracea, H. discoidea, H. fragilis, H. gigas, H. incrassata, H. lacunalis, H. macrophysa, H. micronesica, H. opuntia, H. simulans, H. stuposa,* and *H. taenicola* (Taylor, 1950; Dawson, 1956, 1957). The representation of this genus in the floras of northeastern Australia, Indonesia, New Guinea, the Philippines, the South China Sea and Indochina (Harvey, 1860, 1863; Heydrich, 1892, 1894; Schumann and Lauterbach, 1901; Weber-van Bosse, 1913; Schmidt, 1928; Lucas, 1934; Levring, 1946; Gilbert, 1947; May, 1951; Dawson, 1954), appears very similar, with an average of 10 species known from each. Proceeding northward, the number of species seems to decrease, with *H. cylindracea, H. discoidea, (H.? cuneata), H. incrassata, H. macroloba, H. opuntia* and *H. tuna* found in the regions of Formosa, the Ryukyu Islands, and southern Japan (Okamura, 1907–37; Yamada, 1925, 1934, 1950; Segawa, 1956). Although these areas lie mainly in more temperate latitudes, the tropical element in their floras is not unexpected, since the warm Kuroshio and Tsushima currents flow along the coasts. Along the adjacent mainland, however, in the regions of northern China and Korea, conditions are generally unfavorable for the growth of *Halimeda* because of lower surface water temperatures and decreased salinities. Thus, it is not surprising to find this genus missing from the lists of algae published for these regions.

Of the numerous small island groups of the Pacific, the most extensively and recently studied are the Marshalls (Taylor, 1950, 1953; Dawson, 1956, 1957), the species of *Halimeda* found on them having been enumerated earlier. The genus seems to have a similar representation in the adjacent Gilbert and Caroline Islands (Reinbold, 1901; Okamura, 1904, 1916; Yamada, 1944a, 1944b; Glassman, 1952, 1953; Moul, 1953) of the northern hemisphere, the Ellice Islands (Barton, 1900; Chapman, 1955), and other groups of the southern Pacific, including the Cook Islands, Samoa, and the Tuamota Archipelago (Dickie, 1875, 1876; Reinbold, 1896; Setchell 1926a, 1926b). For many of these however, such thorough collections as exist for the Marshall Islands have not been made.

Only three species, *H. discoidea, H. gracilis,* and *H. opuntia,* can be attributed with certainty to the Hawaiian Islands which are situated towards the northern limit of the tropical range. Their algal flora has been fairly completely studied, the recent workers including Howe (1934) and Egerod (1952); so the small number of species seems to imply the action of other distributional factors, rather than incomplete collection.

A single species, *H. opuntia,* has been reported by Børgesen (1924) for Easter Island, lying below the Tropic of Capricorn, whereas in the narrow belt marked out by the 25 °C isotheres along the western American coast, only *H. discoidea* (frequently reported as *H. tuna*), *H. opuntia,* and possibly *H. tuna* itself seem to occur (Howe, 1911; Setchell

and Gardner, 1920, 1924, 1930; Dawson, 1944, 1946; Taylor, 1945). The plants known for these last three localities are pantropical.

The species restricted to the western Atlantic are *H. favulosa, H. lacrimosa, H. monile,* and *H. scabra.* The first two are of limited occurrence within the region, with *H. favulosa* collected only in the Bahamas, and *H. lacrimosa* in the Bahamas and Cuba. The distribution of *H. scabra,* present in the floras of Florida, Bahamas, South Caicos, and Cuba, is somewhat less restricted. In contrast, *H. monile* occurs throughout the area, and is frequently collected on sand flats, usually growing in close association with sea grasses such as *Thalassia,* or with *H. simulans* and *H. incrassata,* two other members of the *H. incrassata* complex.

Although the intensity of collecting has varied considerably within the region, Harvey (1858), Mazé and Schramm (1870–77), Collins (1901, 1909–18), Collins and Hervey (1917), Howe (1903, 1905a, 1905b, 1907, 1909, 1915, 1918a, 1918b, 1920), Vickers (1905, 1908), Børgesen (1911, 1913), Taylor (1925, 1928, 1933, 1940, 1941, 1943, 1954a, 1954b, 1955), Taylor and Arndt (1929) being the greatest contributors, a diversified population of *Halimeda* is known to exist in the Florida Keys where 8 out of the 10 species known for the Atlantic have been found, with 9 species known for the Bahamas, 8 species for Cuba, and 7 for Jamaica. This genus is also well represented in the floras of Hispaniola, Puerto Rico, the Virgin Islands, and Guadeloupe. The eastern shores of Central America with six species, *H. discoidea, H. opuntia, H. tuna, H. monile, H. simulans,* and *H. incrassata* present a marked contrast in diversity as compared to the western shores where only the first two or possibly three of these species are known to occur.

Within the Gulf of Mexico where there is considerable drainage from rivers and accumulation of mud, a somewhat impoverished flora exists, with *H. opuntia, H. monile* and *H. incrassata* being the only known representatives of the genus. The floristics of the Gulf and of the entire area have most recently been dealt with by Taylor (1954a, 1954b, 1955).

Bermuda, situated outside of the Caribbean and considerably north of the Tropic of Cancer, lies in the path of the Gulf Stream. The temperature of its surface waters is sufficiently warm to sustain a tropical flora, this having Caribbean affinities and including *H. monile, H. simulans, H. incrassata,* and *H. tuna* (Dickie, 1877; Collins and Hervey, 1917; Bernatowicz, 1952, 1953). Noteworthy is the absence of *H. opuntia.*

Extensive collections have not been made along much of the tropical Atlantic coast of South America. There are, however, several lists of algae for this region including those of Dickie (1874b, 1874c), Möbius (1889), Piccone (1889), Schmidt (1924), Howe (1928), Taylor (1930) and Williams and Blomquist (1947). The flora has been analyzed by Taylor (1931) as possessing certain Caribbean affinities, the members of this genus collected in northern Brazil being *H. discoidea, H. simulans, H. opuntia,* and *H. tuna.* The last two have been reported for as far south as Cabo Frio and Rio de Janeiro.

As an adjunct to the Atlantic, the Mediterranean is almost entirely isolated from other tropical floras, the possibility of the introduction of species from the Indian Ocean through the Suez Canal by natural methods having been found unlikely (Lyle, 1930). The affinities of its flora (Feldmann, 1937) are temperate and subtropical to tropical, the perennial *H. tuna* being one of the conspicuous elements of the latter. Although this is the only species of *Halimeda* represented for the Mediterranean, its distribution is ex-

tensive, ranging from Israel to Tangiers. Elsewhere on the eastern Atlantic coast this species has been reported from the Canary Islands, and *H. discoidea* (misnamed *H. tuna*) from the Cape Verde Islands (Dickie, 1874a; Barton, 1897; Børgesen, 1925).

Although the genus is in general restricted to the tropical zone as defined by 23° north and south latitude, its distribution more closely parallels the occurrence of warm water. Thus, in the regions of Florida, Bermuda, and Japan, Halimedae occur in temperate latitudes, whereas along the Pacific Coast of America and to a somewhat lesser extent the western shores of Africa, they are confined to a relatively narrow band within the tropics. On the fringes of this range it seems likely that a limited amount of adaptation to cooler temperatures occurs. Only two species however, *H. cuneata* and *H. tuna*, seem capable of extensive development in subtropical waters, the former appearing to be almost entirely restricted to this temperature province, whereas the latter exists primarily within tropical regions, but in the Mediterranean is able to withstand the relatively cool winter temperature of the water.

In vertical distribution these plants may be classified as sublittoral, extending from just below low tide-line to 80 meters depth (*H. opuntia*), with *H. bikinensis*, *H. cylindracea*, *H. gigas*, *H. gracilis*, and most plants of *H. lacunalis* known only from deep water (to 55 meters depth). Specimens of *H. opuntia*, *H. favulosa*, *H. incrassata*, and most particularly *H. monile* may be exposed at low tide, such plants receiving little protection from the sun. Unlike many algae, Halimedae are capable of colonizing sand and mud flats, their fine rhizoids interweaving among the particles of the substratum and eventually developing into compact holdfast structures. In the Caribbean, such unconsolidated areas are typically colonized by members of the *H. incrassata* complex, these generally occurring in close association with one another and with sea grasses such as *Thalassia*. Substrate requirements vary, however, and other species such as *H. scabra* and *H. tuna* are usually found attached to stones, also sometimes becoming exposed at low tide, whereas *H. opuntia* occurs in rocky or sandy areas, and often forms massive carpets on the bottom to the exclusion of all other algal species (Børgesen, 1900). Since this species is common in dredge hauls in the western Atlantic its absence from Bermudan waters is remarkable. It is also a conspicuous element in the lagoons of many of the Pacific atolls including the Marshall Islands (Taylor, 1950). Here, at between approximately 45–65 meters depth, living plants form a thin mat over a floor of *Halimeda* debris, this latter being the dominant element in sediments from the outer slopes of the atolls to over 360 meters (Emery, 1948; Emery *et al.*, 1949). Similar results were obtained in the borings at Funafuti in the Ellice Islands. Finckh (1904) in reporting these, lists *Halimeda* as being second in importance in coral reef formation, followed by the Foraminiferae and finally the corals, the greatest contributors being the Lithothamneae (nullipores).

Although temperature within the tropical zone is not a major distributional factor for Halimedae, it is nevertheless correlated with the growth cycle of the plants. For *Halimeda* in general, the peak in numbers of individuals seems to be attained at the time of temperature and light maxima or shortly thereafter (Bernatowicz, 1952, 1953; Chihara, 1956). Conflicting opinions have been expressed as to a similar correlation between temperature and the occurrence of reproductive individuals, Chihara (1956) explaining the presence of fruiting plants found on the Izu Archipelago in late June and on the more northerly Kzu Peninsula a month later on this basis. Howe (1915), having collected fertile specimens of *H. incrassata* in March, July, and November in the Carib-

TABLE 1

Times of occurrence of gametangia for various species of *Halimeda*

	J	F	M	A	M	J	J	A	S	O	N	D
Pacific—Japan—northern	....	....	....	....	....	....	*? cuneata*	....	....	....	....	....
southern	....	....	....	....	....	*? cuneata*	....	....	....	....	....	....
Hawaiian Islands	....	....	....	....	....	....	....	....	....	....	....	*discoidea*
Philippines	....	....	*tuna*	....	*macroloda*	....	*opuntia*	....	*opuntia*	....	....	....
Indonesia	....	....	....	....	....	....	....	*macroloba*	....	....	....	....
Atlantic–Florida	....	....	*scabra*	....	*incrassata*	*incrassata*	*scabra*	....	....	....	....	....
							simulans					
Bahamas	....	*favulosa*	....	....	....	....	....	....	....	....	*incrassata*	*incrassata*
Greater Antilles	....	....	....	....	....	....	....	....	....	....	....	*monile*
Puerto Rico	....	*discoidea*	*incrassata*	....	....	....	*incrassata*	....	....	....	....	....
			tuna									
Lesser Antilles	....	....	....	*incrassata*	....	....	....	....	....	....	....	....
Mediterranean—	....	....	....	....	....	*tuna*, small-segmented plants			....	....	....	....
(data summarized)	....	....	....	....	....	....	....	....	*tuna*, large-segmented plants			....

bean felt that temperature could not be the controlling factor. Table 1 summarizes the information available on the months in which fertile individuals have been collected, the data coming from herbarium specimens and published records. From this it would appear that there is generally no correlation with water temperature. In the Mediterranean, Funk (1927) designated the fruiting period of *H. tuna* with small segments as June to August, and of deep water plants with large segments as September to November. Since the winter water temperatures here are somewhat lower than those normally encountered by tropical plants, temperature may prove to be an important factor in inducing sexual reproduction of *Halimeda* in the Mediterranean.

Systematic Treatment

The aim of taxonomists centers in the recognition of species. The exact delimitation of this unit, however, which is so basic to biological thought, has perplexed workers since the question "What is a species?" was first posed. The value of various morphological and anatomical criteria as tools in ascertaining relationships has been recognized, their usefulness being a function of the inherent variability. Thus, for flowering plants, characteristics of the reproductive structures have generally proved more reliable than those of the vegetative organs. Within the genus *Halimeda,* however, the latter must be used almost entirely. The details of structure have been discussed in an earlier section; so the following discussion deals mainly with the usefulness as taxonomic criteria of characteristics of habit, segment morphology, the cortical layers, nodal anatomy, reproduction, and geographical distribution.

Habit, although distinctive for certain species, is of limited value. Included, in addition to general form, is the extent of development of the stipe and the holdfast. The degree of branching is often a reflection of the environment, and in such cases is not taxonomically pertinent.

The morphology of the segment is extremely variable, with several shapes commonly occurring on the same specimen. The extent of variation for any one species, however, is restricted and often is sufficiently narrow for shape to be of taxonomic value. Color is correlated with the extent of calcification. Its estimation is somewhat subjective. Size, although sometimes characteristic for the species, often shows environmental response.

The surface diameters of the peripheral utricles and to a lesser extent the number supported by each secondary utricle are of taxonomic importance, whereas the lengths of both the peripheral and secondary utricles, the degree of adherence of the former after decalcification, and the extent of development of the cortical layers, in most species vary ontogenetically. The diameters of the utricles of the inner cortex may be useful, but are somewhat influenced by the number of layers of utricles.

The behavior of the medullary filaments at the node, when restricted to three general categories: that of remaining separate, of fusing in small groups, and of uniting into a single unit, seems fairly constant for the various species. This feature is more valuable, however, in delimiting groups of species rather than individual species. The presence of detectable amounts of callose in the walls of these filaments has been considered important in segregating genera within the Siphonales (Feldmann, 1946, 1951).

Since the majority of the specimens collected are sterile, fruiting characteristics at most will serve to support identifications. When such structures are known in detail for

more species, the size of the gametangia and the manner in which the gametophores arise from the segments may prove diagnostic.

Geographical distribution is useful as confirmatory evidence, but should be employed only in conjunction with other criteria, as should any ecological data, such as the depth at which the plants were obtained, or the type of substratum.

In Barton's systematic treatment of the genus (1901) no reference was made to the four sections established by J. Agardh in 1887. These were based on differences of habit and segment morphology, the resulting system being neither natural nor particularly useful since the groups delimited represent for the most part rather poorly defined habit types. Furthermore, Agardh's scheme did not take cognizance of the extreme variability of segment morphology, the result being that different aspects of the same species were classified in different sections. In view of the above criticisms, simple modification of this system, with the subsequent establishment of new sections to accommodate certain species, does not seem justified.

In the subsequent systematic treatment, species which seem closely related have been grouped within the framework of two main categories referred to as the *H. tuna* and *H. incrassata* complexes. These delimit the taxa according to two of the three main types of medullary filament behavior at the node. Thus, species in which the filaments fuse into small units are referred to the *H. tuna* complex, those in which the nodal filaments unite into a single group to the *H. incrassata* complex. This system is believed to represent a more natural approach, with four basic types, *H. discoidea*, *H. gracilis*, *H. opuntia*, and *H. tuna* possibly existing within the *H. tuna* category. From histological evidence, the affinites of *H. lacrimosa* would seem to lie nearest to *H. gracilis*, those of *H. cuneata*, *H. lacunalis*, *H. gigas*, and *H. scabra* to *H. tuna*. The *H. incrassata* complex represents a fairly compact unit, *H. favulosa* being the most modified.

In outlining such a system, the treatment of *H. fragilis* and *H. micronesica*, the two species having the third type of nodal structure (i.e., the medullary filaments remaining separate throughout the node), is more problematic. One solution would be their delimitation as a separate category. Although this would be useful, such an approach may be quite artificial since anatomical evidence also suggests the possibility of *H. opuntia* or *H. incrassata* as progenitors. Further elucidation of phylogenetic relationships or any formal delimitation of taxonomic categories such as sections should await the availibility of larger collections of *H. fragilis* and *H. micronesica*.

Generic Description

Halimeda Lamouroux, 1812

Halimedea Lamouroux, 1812, p. 186.

Halimeda Lamouroux, 1816, p. 302, *nomen conservandum*.

Ormus Hill, 1751, p. 12, Plate 3.

Sertularia Boehmer *ex* Ludwig, 1760, p. 504.

Corallina p.p. Linnaeus, 1758, p. 805; Pallas, 1766, p. 420; Petiver, 1767, Plate 20, Figure 19; Ellis and Solander, 1786, p. 108; Esper, 1798–1806, Plate 11.

Flabellaria p.p. Lamarck, 1813, p. 302; Delle Chiaie, 1829, p. 9, Plate 10.

Fucus p.p. Bertolini, 1819, p. 224, p. 316.

Ulva p.p. Pollinius, 1824, p. 507.

Codium p.p. Sprengel, 1827, p. 366.

Opuntia p.p. Naccari, 1828, p. 104.
Sertolara Nardo, 1834, p. 673.
Botryophora Bompard, 1867, p. 129.

Plants flaccid, prostrate or erect, and generally bushy, arising from a filamentous holdfast system, usually not exceeding 25 cm in height although to over 40 cm in some lax or prostrate specimens; branches composed of linear series of calcified internodes or segments, the nodes being uncalcified and flexible; segments plane or ribbed, spherical, tear-shaped, compressed-cylindrical, or cuneate to reniform in shape, with the upper margins entire or lobed; organization consisting of coenocytic filaments, these producing a multiaxial core of medullary filaments surrounded by a cortex composed of layers of utricles, the outer walls of the peripheral utricles forming a continuous or slightly discontinuous surface; the medullary filaments remaining separate, or anastomosing in small groups, or into a single large unit at the nodes, their walls generally thickened in these regions; reproduction by biciliate gametes produced in large globular to pyriform gametangia on stalks which are simple or branched, and arise from the segment margin or surface.

Lectotype species: Halimeda tuna (Ellis and Solander) Lamouroux.

Key to Species

1. Holdfast usually well-developed, rarely less than 1 cm long and frequently massive; nodal medullary filaments uniting as a single group, the adjacent filaments communicating by pores (Plate 7, Figures 11, 13); plants often growing in sand or mud 15
1. Holdfast rarely exceeding 1 cm in length; nodal medullary filaments remaining separate or uniting in twos, threes and occasionally fours; plants frequently attached to rocks or stones, or forming massive beds 2

2. Holdfast region not restricted to the initial area; branching generally in more than one plane ..... *H. opuntia*, p. 359
2. Holdfast single and more conspicuous; branching essentially in one plane 3

3. Habit flaccid, straggling, decumbent; segments relatively small, generally less than 9 mm long, 15 mm broad 4
3. Habit erect or prostrate but not flaccid; segments small or large, to 29 mm long, 42 mm broad 5

4. Plants small, not exceeding 5 cm in length; at least the segments of the upper half of the plant spherical or tear-shaped ..... *H. lacrimosa*, p. 357
4. Plants to over 40 cm long; segments subcylindrical or flat; known only from deep water ..... *H. gracilis*, p. 356

5. Basal segment flabellate, supporting numerous branches ..... *H. micronesica*, p. 364
5. Basal segment not specialized 6

6. A small "cushion" segment (to 1.5 mm long, 5.5 mm broad) interposed between some or all of the segments (Plate 1, Figure 6) ..... *H. cuneata*, p. 345
6. Small "cushion" segments absent 7

7. Average surface diameter of the peripheral utricles exceeding 120 microns 8
7. Average surface diameter of the peripheral utricles less than 120 microns 9

8. Segments large, to 25 mm long, 42 mm broad; color on drying brownish-green; calcification rather light; not friable ..... *H. gigas*, p. 350
8. Segments smaller, to 15 mm long, 24 mm broad; color on drying white or pale greenish-white; calcification moderate; friable ..... *H. macrophysa*, p. 351

9. Peripheral utricles each projecting into a central spine ..... *H. scabra*, p. 348
9. Peripheral utricles smooth 10

10. Peripheral utricles separating spontaneously, or with slight pressure on decalcification 11
10. Peripheral utricles remaining firmly attached after decalcification 12

11. Segments relatively large, to 16 mm long, 25 mm broad, predominately reniform or subreniform; habit spreading, to 20 cm tall; nodal medullary filaments fusing in twos and threes ..... *H. bikinensis*, p. 358
11. Segments smaller, to 8.5 mm long, 16 mm broad, reniform to trilobed; habit compact, often cushionlike, to 8 cm tall; nodal medullary filaments remaining separate ..... *H. fragilis*, p. 363

12. Peripheral utricles generally 50 microns or less in surface diameter ..... *H. lacunalis*, p. 349
12. Peripheral utricles generally exceeding 50 microns in surface diameter 13

13. Secondary utricles noticeably inflated, generally exceeding 90 microns in breadth (Plate 6, Figure 11) ..... *H. discoidea*, p. 352
13. Secondary utricles less than 90 microns broad 14

14. Segments, at least those of the upper half of the plant, predominantly reniform, averaging 0.50–0.77 mm in thickness ..... *H. tuna*, p. 342
14. Segments, particularly those of the upper half of the plant, most commonly subcuneate or trapezoidal, averaging 1.0–1.5 mm in thickness, the surface often becoming concave on drying ..... *H. taenicola*, p. 354

15. Segments large, broad, flat, to 29 mm long and 40 mm broad *H. macroloba*, p. 375
15. Segments smaller, flat or cylindrical, to 12 mm long and 16 mm broad (excluding basal or fusion segments) 16

16. Segment surface appearing pitted when viewed macroscopically; peripheral utricles generally exceeding 110 microns in surface diameter—*H. favulosa*, p. 370
16. Segment surface not appearing pitted when viewed macroscopically; peripheral utricles generally less than 100 microns in surface diameter 17

17. Segments of the upper half of the plant, except those supporting branches, predominantly cylindrical, the length usually at least four times the diameter 18
17. Segments of the upper half of the plant flat, or if cylindrical the length usually not more than twice the diameter 19

18. Diameter of the cylindrical segments remaining fairly constant from base to apex of the plant, averaging 1.0–1.5 mm; stalk short, of 1–2 segments ..... *H. monile*, p. 371

18. Diameter of the cylindrical segments decreasing from base to apex of the plant, averaging 3–4 mm near the base, and 1.0–1.5 mm towards the apex; caulescent, or in older plants with a number of these cauline structures somewhat consolidated laterally into a basal fan-shaped structure ..... *H. cylindracea*, p. 373

19. Plants thick-set in appearance, the segments averaging 2 mm in thickness; segments subcuneate to cylindrical, often becoming subspherical towards the plant apex ..... *H. stuposa*, p. 374

19. Plants not appearing thick-set, the segments (excluding the basal ones) averaging 0.75–1.00 mm in thickness; segments generally subcuneate to reniform ... 20

20. Peripheral utricles generally 50 microns or less in surface diameter; segments predominantly subcuneate to reniform with the outer margin entire to shallowly lobed; plants to 10 cm tall ..... *H. simulans*, p. 368

20. Peripheral utricles generally exceeding 50 microns in surface diameter; segments cylindrical to reniform with the outer margin often deeply lobed; plants to 24 cm tall ..... *H. incrassata*, p. 365

Halimeda tuna (Ellis and Solander) Lamouroux

Plate 1, Figures 4–5; Plate 5, Figure 9; Plate 6, Figure 7; Plate 9.

Corallina tuna Ellis and Solander, 1786, p. 111, Plate 20, Figure e.

Halimedea tuna Lamouroux, 1812, p. 186; *Halimeda tuna* Lamouroux, 1816, p. 309, Plate 11, Figure 8; Barton, 1901, p. 11, Plate 1, Figures 1–6; Mazza, 1904, p. 147; Collins, 1909–18, p. 400; Taylor, 1928, p. 85; Hamel, 1931, p. 407, Figure 26.

?*Halimeda tuna* f. *albertisii* Piccone, 1879, p. 23, Figure 2; Barton, 1901, p. 14, Plate 1, Figure 3.

Halimeda tuna f. *platydisca* (Decaisne) Barton, 1901, p. 14, Plate 1, Figure 2; Gilbert, 1947, p. 124. *Halimeda platydisca* Decaisne, 1842, p. 102.

Halimeda tuna v. *platydisca* Børgesen, 1911, p. 134; Børgesen, 1913, p. 106; Collins, 1909–18, p. 102; Taylor, 1928, p. 85, Plate 10, Figure 13.

Plants spreading or compact, often forming cushion-like clumps, arising from an inconspicuous holdfast, to 15 cm tall; calcification moderate to light, sometimes becoming heavier towards the base; color on drying rusty-brown or cream, to white or greenish; the surface dull or somewhat glossy; branching generally ditrichotomous; basal segments often subcuneate, the others plane or sometimes ribbed, mainly subcuneate, discoid or reniform, commonly relatively small, to 13 mm long, 19 mm broad, and averaging 0.50–0.75 mm. in thickness, but in other specimens, often from deep water, to 25 mm long and 40 mm broad.

Cortex of two to four layers of utricles; outermost utricles remaining firmly attached after decalcification for a distance of approximately 12–16 microns, sometimes fusing laterally in twos or threes for this same distance; lateral and peripheral walls occasionally somewhat thickened; unfused peripheral utricles measuring (25–)34–100 (–125) microns in surface diameter, (46–)60–130(–230) microns long in section, two to four or occasionally up to seven supported by each secondary utricle; secondary utricles (20–)30–80(–110) microns broad; tertiary utricles 40–130 microns broad.

Nodal medullary filaments united in twos and threes, the length of fusion usually 1.5

or several times the filament diameter; resultant units usually densely entangled and remaining separate or laterally adhering for an average distance of 85 microns.

Type locality: Mediterranean Sea. This species is the type for the genus.

Ecological and geographical distribution: Extending from near lowtide level to over 80 meters depth in tropical and somewhat subtropical waters; common in rocky areas; known for the Atlantic, Pacific, and Indian Oceans, and is apparently the only species of the genus represented in the Mediterranean.

Representative specimens examined: MEDITERRANEAN SEA. PALESTINE, Bat-Yam, Bursa, 30 March, 1945 (NY); Israel, Rayss, 22 August, 1951 (UC 954921). GREECE, Psythalia Island near Athens, Schmitz, 1878 (UC 74695). TRIESTE, Anon., *ex* herb. Hauck (NY). ADRIATIC SEA, Schiller 50, 6 March, 1911 (BM, NY); Bagnole Island, Brunnthaler, September, 1911 (BM); Lessina, Botteri, 8 April, 1844 (UC 434125, as *Flabellaria tuna*). ITALY, Gulf of Naples, Brunnthaler, 22 April, 1914 (MICH, UC 413875); Geneva, Schimper and Wiest, 2 November, 1934 (NY); Capri, Davis, May, 1904 (MICH). ELBA ISLAND, Toscanelli 1442 (BM, NY). CORSICA, Børgesen, November, 1897 (NY). SARDINIA, Marcucis, 1866 (UC 435651). FRANCE, Antibes, Anon., *ex* herb. Farlow (NY); Marseilles, Anon. (BM); Banyuls, Feldmann 1802, 27 August, 1931 (NY). SPAIN, Lindahl 340, autumn, 1870 (NY).

ATLANTIC OCEAN. BRAZIL, Barro Grande, Moseley (BM). PANAMA, Caledonia Harbor, Taylor 39–239, 4 April, 1939 (MICH). BRITISH HONDURAS, Punta Negri, Schipp A 119b, 9 May, 1933 (MICH, as *H. simulans*). MEXICO, Yucatan, Schott 785, 10 November, 1865 (WRT). BARBADOS, Vickers 42, 18 March, 1903 (NY). GUADELOUPE, Questel 10213, 1 November, 1944 (WRT). VIRGIN ISLANDS, Børgesen 1763, 1905–06 (NY). PUERTO RICO, Howe 4201, 3 March, 1906 (NY, fertile). HAITI, Arndt, 2 April, 1927 (WRT). SOUTH CAICOS, Howe 5595, 16 December, 1907 (NY). JAMAICA, Taylor 56–255, 30 March, 1956 (WRT). CUBA, Howe 6466, 24 March, 1909 (NY). BAHAMAS, Howe 5379, 6 December, 1907 (NY). FLORIDA, Curtiss, September, 1895 (NY). BERMUDA, Taylor and Bernatowicz 49–940, 25 April, 1949 (MICH). CANARY ISLANDS, d'Orbigny, 1842 (NY, TYPE for *H. platydisca*).

PACIFIC OCEAN. PHILIPPINES, Sulu Archipelago, Bartlett 16034, 15 September, 1935 (MICH); Williams, 21 March, 1905 (NY, fertile). MALAYA, Singapore, Beccari (NY, as *H. papyracea*). LESSER SUNDA ISLANDS, Bali, Pullai BB 382 in part, July, 1933 (UC 624482). JAVA, Kostermans 362, 6 October, 1938 (MICH). TONGA ISLANDS, Graeffe (BM). NEW CALEDONIA, Buchholz 1779, 15–16 March, 1948 (UC 767338).

INDIAN OCEAN. AMIRANTE ISLAND, Gardiner (in part), 9 October, 1905 (BM). SEYCHELLES ISLANDS, Coelivy Island, Gardiner, 20 October, 1905 (BM). AFRICA, Zanzibar, Stuhlmann 1205a (BM). GULF OF ADEN, off Alula, John Murray Expedition, 12 October, 1933 (BM). CEYLON, Ferguson 67 (BM). SAYA DE MALHA, Gardiner (BM). CARGADOS CARAJOS SHOALS, Gardiner (BM). MAURITIUS ISLAND, Robillard, 1881 (BM).

The early synonymy of *H. tuna*, its nomenclatorial history dating back to 1599, is given by Barton (1901).

This species which was first described for the Mediterranean, has subsequently been attributed to most tropical areas. The specimens from these other regions, however, usually differ in one or more respects from the small-segmented Mediterranean plants

which constitute the author's concept of the type. In the ensuing description and evaluation of these variations in specimens from different areas, plants with relatively small segments, usually not exceeding 13 mm in length and 19 mm in breadth, and those with larger ones, to 25 mm long and 40 mm broad, the latter often identified as f. *platydisca*, are discussed separately.

In habit, the typical Mediterranean plants seem rather small and cushion-like, whereas the specimens with small segments from the Atlantic and Indian Oceans are larger, and somewhat less compact. A conspicuous feature in older plants from these latter two regions is the occurrence of segments which were probably produced during two or three separate growing periods, with the lower segments often golden-colored, more heavily calcified, and in western Atlantic specimens commonly subcuneate in shape. Accompanying this modified appearance of Atlantic and Indian Ocean plants are certain variations in histological characteristics. These include a decrease in the diameters of the peripheral utricles which average approximately 50 microns in surface view, as opposed to 65 microns for the typical plant, and a greater regularity in their surface appearance with an apparent absence of lateral fusions. Their peripheral walls also tend to become thickened. In addition, the height of the peripheral and secondary utricle layers is somewhat greater, this together with the decreased diameters of the outer utricles creating a vertical rather than a "V"-shaped appearance in sagittal section. As an additional point of difference, the units formed by extended fusion of the nodal filaments usually adhere laterally for an average distance of 85 microns in plants from the western Atlantic and Indian Oceans, whereas in the typical plants both short and extended fusions commonly occur, the resultant units usually remaining separate or, at most, adhering only slightly.

In external appearance, plants of this species with large segments can be segregated into three groups: (1) those of the Atlantic and Indian Oceans that usually have pale-greenish and relatively thin segments, (2) Mediterranean plants with somewhat smaller, bright or dark green, and often thick and leathery segments, and (3) Pacific Ocean specimens of greenish-white segments, the outer margins of which are commonly conspicuously undulated or folded. Histologically, all three groups resemble the typical plant rather than the Atlantic and Indian Ocean small-segmented specimens, with members of the first group seeming very similar to the type specimen of *H. platydisca*. This latter plant was collected by d'Orbigny in the Canary Islands and has been deposited in the herbarium of the Muséum National d'Histoire Naturelle in Paris. From a study of a photograph of this type and an examination of the small fragment of it in the New York Botanical Garden Herbarium, *H. platydisca* does not appear to differ significantly from the typical *H. tuna*, a conclusion which was also reached by Barton (1901) and Howe (1907). In plants of the second and third groups, however, the diameters of the peripheral utricles, surface view, are greater, these averaging 80 microns in Mediterranean plants and 90 microns for the Pacific specimens, as opposed to 65 microns for the typical plants and those of the first group. The Pacific plants with large segments also differ in that two rather than three cortical layers commonly occur in mature segments. The appearance of the latter specimens, the outer margin of their segments usually undulated or folded, is suggestive of Barton's drawing of *H. cuneata* f. *undulata* (1901, Plate 1, Figure 10), the exact identity of which is not known at the present time. However, it seems unlikely that these can be the same, since the average surface diameter of the peripheral utricles of *H. cuneata* f. *undulata*, as given by Barton,

is 38 microns, and hence considerably smaller than that of the Pacific plants. In this description of five elements within *H. tuna*, the average surface diameters of the peripheral utricles have indeed been useful in indicating differences. Nevertheless, there is sufficient overlap in range of measurements to preclude for this species a satisfactory separation on this basis alone.

It is always difficult to evaluate correctly the effect of environment on a plant. The study of the Mediterranean plants with small and large segments would seem to indicate that variations in segment size and peripheral utricle diameters in this species are largely environmental. Consequently, plants differing only in these characteristics have not been given separate taxonomic standing. The Pacific specimens with large segments show additional modifications, but do not seem sufficiently different from the typical *H. tuna* to warrant segregation as a separate taxon at this time. A further development of these variations seems embodied in *H. gigas*, which has been maintained as a distinct species for the reasons given in its taxonomic treatment.

In comparing the specimens with small segments, it is tempting to consider those of the Atlantic and Indian Oceans as distinct from the Mediterranean plants. It seems likely, however, that the latter, although considered closest to the type, may actually represent a modified condition. Such might develop as an adaptation to the colder winter water temperatures of the Mediterranean, these temperatures being more extreme than those generally found in the tropical zone. Preliminary culture experiments on the Mediterranean *H. tuna* by Techet (1908) give some information regarding the influence of the environment, and the photograph included in his paper showing the habit of plants subjected to reduced salinity is suggestive of Caribbean specimens and of Piccone's f. *albertisii*. More insight into the possible effects of environment, in this case of temperature, is given by the observation of Howe (1905a), that specimens from Bermuda, a region at the extreme of the tropical range delimited by the 25°C isothere, resemble the Mediterranean *H. tuna* more closely than do Caribbean plants. This statement is amply supported by herbarium specimens. These indications of the effect of environment have led to considering the Atlantic and Indian Ocean small-segmented plants, and probably also f. *albertisii*, although the type specimen was not seen, as within the limits of the typical *H. tuna*.

In the preceding discussion of the plants of *H. tuna* with small segments, no reference was made to such specimens from the Pacific. It seems likely that these, at least to a certain extent, are embodied in *H. lacunalis*, a species which shows certain similarities to the *H. tuna* of the Atlantic and Indian Oceans.

Halimeda cuneata Hering

Plate 1, Figure 6; Plate 5, Figures 1–2; Plate 6, Figure 10; Plate 7, Figure 7; Plate 9.

Halimeda cuneata Hering *in* Krauss, 1846, p. 214; Barton, 1901, p. 15, Plate 1, Figure 7, but not Plate 1, Figure 9, or Plate 2, Figure 10.

Halimeda obovata Kützing, 1858, p. 11, Plate 25, Figure 1.

Halimeda versatilis J. Agardh, 1887, p. 86.

Plants rather loosely organized or occasionally compact, arising from a small but distinct holdfast region, to 25 cm tall; calcification light; color on drying greenish to cream, the surface smooth and usually somewhat glossy; branching mainly dichot-

omous but with up to six segments arising from a single one; the basal first to second segments cylindrical to subcylindrical, often giving the appearance of a short stipe; other segments plane, mostly cuneate to subcuneate, sometimes discoid, generally to 16 mm long, 18 mm broad and averaging 0.50–0.75 mm in thickness, but in some specimens reaching 21 mm in length and 27 mm in breadth; many of the segments supported by a cushion segment, to 1.5 mm long, 5.5 mm broad, or a stalk region of uncorticated medullary filaments, or both.

Cortex of two to four layers of utricles; outermost utricles remaining firmly attached after decalcification for an average distance of 35 microns, occasionally fusing laterally in pairs for this same distance; unfused peripheral utricles 25–63 microns in surface diameter, 58–100(–135) microns long in section, usually four but occasionally two supported by each secondary utricle; secondary utricles 20–55(–66) microns broad, 20–67 microns long; tertiary utricles (40–)50–80(–94) microns broad.

Nodal medullary filaments united in twos and threes, the length of fusion usually 1.5 or several times the filament diameter; fused units densely entangled, but at most adhering only slightly; filament walls thickened and pigmented in this area, and in the cushion joint and stalk region.

Type specimen: Collected by Krauss at Durban (Natal Bay), South Africa. The label pencilled by Barton on a specimen in the British Museum indicates that it was obtained by Krauss from Natal, but whether it is part of the type collection is unknown. No more certain material has been located.

Ecological and geographical distribution: Frequently growing attached to rocks; known with certainty mainly from the subtropical waters of the Indian and western Pacific Oceans in the southern hemisphere. This species occurs along the southeastern coast of Africa, the southwestern coast of Australia, and on Lord Howe Island off the southeastern coast of Australia. In the literature, *H. cuneata* is often incorrectly reported for much of the tropical Indian and western Pacific Oceans. The specimens examined from these localities commonly proved to be *H. discoidea.*

Representative specimens examined: PACIFIC OCEAN. LORD HOWE ISLAND, MacDonald, 1855 (BM).

INDIAN OCEAN. AFRICA: Cape Province: Cape of Good Hope, Anon., *ex* herb. Averill (NY); Becker (BM); Anon., *ex* herb. Dickie (BM). East London, Duthie 8384, July, 1933 (UC 574344). Port Alfred, Carr 95 (BM); Setchell, 5 May, 1927 (UC 313453). Port Elizabeth, Farquhar, 1893 (BM); Spencer (BM); Lowe (BM, fertile). Algoa Bay, Sutherland, 1885 (BM); Tyson 56 (NY, UC 688164). Jeffrey's Bay, Duthie 8383. July, 1927 (UC 574345). South Africa, Becker, 14 February, 1894 (NY); Krauss, 1839 (BM). Natal: Durban, Evans, 19 January, 1894 (BM); Anon., *ex* herb. Merrifield (BM); Anon., *ex* herb. Pike, 1870 (NY). MADAGASCAR: Waters (BM). AUSTRALIA: Western Australia: Fremantle, Harvey 562 (BM, as *H. macroloba,* ISOTYPE material of *H. versatilis*). Point Peron, Smith, 15 August, 1950 (WRT, as *H. macroloba*). West Australia, Clifton, 1857 (BM); Markwell, 1897 (BM).

This species differs from all other members of the genus in the occurrence of "stalked" as opposed to "sessile" segments, the stalk consisting of either a small cushion segment, or a stalk region or both. The medullary filaments, subsequent to fusion in twos and threes in the node region of a typical segment, extend into the cushion segment which consists of cortical layers as in a regular segment, although the inner layers are usually not as regular in appearance or as extensively developed. In cushion segments near the

base of the plant, however, the cortex may be replaced by rhizoidal filaments, such segments being readily recognized by their looser, rather disorganized appearance. The walls of the main filaments in the cushion segments and often of their branches are somewhat indurated. This is evident not only in section but also in a surface view of the peripheral utricles, although care must be taken in the latter to distinguish between actual thickening and a somewhat similar appearance which may occur in regular segments, but which is usually the result of a shrinkage of the material occasioned in its initial drying. At the apex of these cushion segments, the medullary filaments commonly branch dichotomously, but may also remain unforked. In either case they usually become torulose and proceed uncorticated for some distance. This region represents the stalk. These filaments ultimately branch, generally trichotomously, their rami developing into the cortical layers of the new segment.

The preceding account describes the complete expression of the "stalk" region between segments. The extent of its development varies with the individual specimen and may to a limited degree be influenced by age, since it was rather uncommon in the few young plants observed. Rarely, however, does a plant occur without either of these structures being interposed between some of its segments.

A second fairly prominent characteristic of *H. cuneata* is the extensive attachment of adjacent peripheral utricles which is for approximately 0.3–0.5 of their length. Such, however, is not unique for this species, these utricles also adhering for a considerable distance in *H. discoidea*, and for somewhat shorter distances in *H. tuna*, and *H. incrassata*. When working with dried material, this region is generally compressed, with the result that in surface view these utricles may present the illusion of being thick-walled.

The concept of this species as maintained by Barton was broad, and included both "stalked" and "sessile" plants within its confines. Since the extent of attachment of peripheral utricles was the main criterion used in addition to medullary filament behavior at the node, many specimens of *H. discoidea* were included, the reported range of distribution of *H. cuneata* thus being considerably extended as has been noted by Gilbert (1947), Papenfuss and Egerod (1957), and the author.

Two forms of this species, f. *digitata* and f. *undulata*, have been designated (Barton, 1901, p. 16, Plate 1, Figure 9; Plate 2, Figure 10), the type specimens of which have not been seen. However, since these are based on "sessile" plants, such not being included in the present concept of the genus, it would seem that they are no longer applicable to *H. cuneata*. The figures given for f. *digitata* and f. *undulata* show considerable resemblance to certain Pacific specimens of *H. discoidea* and *H. tuna*, respectively.

The segments of this species, when compared to the extremely variable ones of *H. opuntia* or *H. incrassata*, seem remarkably uniform. Nevertheless, on the basis of segment morphology and habit, the specimens observed fall into three main types. The typical group and the commonest, includes rather elongate, sparingly branched plants with predominantly cuneate to narrowly subcuneate segments, their length generally exceeding their width. The second type consists of fairly compact plants with thinner, somewhat smaller segments which are subcuneate to discoidal. Plants of the third group are quite similar in habit to the first, but their broadly cuneate segments are considerably larger, to 21 mm long and 27 mm broad, as opposed to 16 mm long and 18 mm broad. The Australian plants studied were of this third type, as was also a tide pool specimen from South Africa. Since the histology of the plants in the three groups does not differ significantly, they have been considered as probably representing environmental modifications, and have not been given taxonomic rank.

Halimeda scabra Howe

Plate 1, Figure 2; Plate 5, Figure 5; Plate 6, Figure 4; Plate 8, Figures 9–11; Plate 9.

Halimeda scabra Howe, 1905a, p. 241, Plates 11 and 12; Collins, 1909–18, p. 401; Taylor, 1928, p. 84, Plate 10, Figures 9 and 10, 18; Plate 11, Figure 22.

Plants generally compact forming cushion-like clumps, or somewhat spreading, occasionally lax and decumbent, in the latter case to 25 cm in length but more commonly not exceeding 9 cm; calcification moderate; color on drying bluish-green, olive or whitish, the surface dull and somewhat rough; branching frequent, usually dichotomous, basal segments often subcuneate; others plane or slightly ribbed, most commonly subreniform to reniform but also subcuneate and discoidal, to 11 mm long, 20 mm broad and averaging 0.50–0.75 mm in thickness.

Cortex of two to three layers of utricles with a fourth zone occasionally present; outermost utricles remaining attached after decalcification, or separating slightly, in the latter case retaining their hexagonal shape as viewed from the surface, each bearing a central indurated spine which may extend to two-thirds the length of the body of the utricle, 26–55(–66) microns in surface diameter, (50–)70–165(–240) microns long in section including the spine, up to seven supported by each secondary utricle; secondary utricles 30–60(–70) microns broad, their length variable and often extending to the medulla; tertiary utricles when present approximately 39–65 microns broad.

Nodal medullary filaments united in twos and threes, the length of fusion approximately 1.5 or several times the filament diameter; resultant units entangled and sometimes adhering for up to 60 microns.

Type specimen: Florida, Sands Key, Howe 2905, 30 March, 1904 (NY).

Ecological and geographical distribution: From near low-tide level to at least 20 meters depth, frequently growing on rocks but also collected at the bases of sponges; of rather restricted distribution in the Caribbean.

Representative specimens examined: ATLANTIC OCEAN. SOUTH CAICOS ISLANDS, Howe 5542, 15 December, 1907 (NY). BAHAMAS, Howe 3216, 15 April, 1904 (NY); Howe 3244, 16 April, 1904 (NY); Howe 3461, 29 January, 1905 (NY); Howe 5811, 24 December, 1907 (NY); Wilson 8122, 21 May, 1909 (NY). FLORIDA, Curtiss, September 1895 (NY, as *H. tuna*); Hooper 41 in Alg. Exsic. Am. Bor., in part (MICH, NY, as *H. tuna*); Dry Tortugas, Taylor 37, 10 June, 1924 (WRT); Dry Tortugas, Taylor 205, 4 July, 1924 (WRT); Dry Tortugas, Taylor 320, 21 July, 1924 (NY, fertile); Key West, Howe 1683, 9 December, 1902 (NY); Caesar's Creek, south of Elliott's Key, Howe 2978, 31 March, 1904 (NY).

In general form and anatomy *H. scabra* seems closely allied to *H. tuna*, particularly to the somewhat modified plants of the Caribbean, and has frequently been identified as such in herbaria. From this species it can often be distinguished macroscopically by the rather bluish cast which commonly occurs towards the apices of the branches, and by the rough texture. The latter results from the indurated spines which project from the peripheral utricles, their length varying to a limited extent with the age of the segment. When well-developed, they are usually visible with low magnification. The relative ease of separation of the peripheral utricles after decalcification, and their small surface diameters are also characteristic for this species, the latter averaging 42 microns in *H. scabra* as opposed to 70 microns in *H. tuna*. Adjacent fused nodal filaments may remain separate, or else adhere for an average distance of 30 microns, whereas in the Caribbean *H. tuna* the filaments are usually attached laterally for an average length of 85 microns.

Halimeda lacunalis Taylor

Plate 1, Figure 1; Plate 5, Figure 6; Plate 6, Figure 13; Plate 7, Figure 8; Plate 9.

Halimeda lacunalis Taylor, 1950, p. 91, Plate 51.

Plants erect or somewhat flaccid, arising from a small holdfast region, to 18 cm tall; calcification light to moderate, frequently becoming somewhat heavier in the basal region; color on drying usually golden to whitish or greenish, the surface often glossy; branching complanate, sometimes sparse, commonly dichotomous but with up to four segments arising from a single one; basal segments often relatively small and subcylindrical to subcuneate; suprabasal segments at times fusing laterally, others occasionally ribbed, most commonly subcuneate or obovate, but also discoidal or reniform, to 15 mm long, 20 mm broad, and averaging 0.50–0.75 mm in thickness.

Cortex of two to four layers of utricles; outermost utricles sometimes thickened towards the periphery, remaining attached after decalcification for an average distance of 13 microns, 20–55(–70) microns in surface diameter, 45–100(–190 microns in subcylindrical segments) microns long in section; two, four, or occasionally five borne on each secondary utricle; secondary utricles 15–50(–60) microns broad, (15–)23–80 microns long, these small utricles absent at times; innermost utricles 35–80 microns broad.

Nodal medullary filaments fusing in twos and threes for a distance of several times the filament diameter; resultant units entangled and adhering strongly for approximately 80–150(–280) microns.

The following two forms within this species have been recognized.

Halimeda lacunalis Taylor f. *lacunalis*

Plants often lax and rather sparsely branched; segments frequently as long or longer than broad, shape mainly cuneate to somewhat obovate, to 15 mm long, 13 mm broad, and averaging 0.5 mm in thickness.

Halimeda lacunalis f. *lata* (Taylor) **n. comb.**

Halimeda gracilis f. *lata* Taylor, 1950, p. 83, Plate 42.

Plants sometimes rather lax, but generally compact; segments usually broader than long, occasionally subcuneate but more generally discoid to reniform, to 15 mm. long, 20 mm broad, and averaging 0.75–1.00 mm in thickness.

Type specimens: Marshall Islands, Eniwetok Atoll, Taylor 46–424, 6 June, 1946 (MICH) for f. *lacunalis*; for f. *lata*, Marshall Islands, Bikini Atoll, Enyu Island, Taylor 46–21, 15 March, 1946 (MICH).

Ecological and geographical distribution: Extending from moderate depths to at least 55 meters, occasionally collected in holes of the reef; known only for the North Pacific.

Specimens examined: PACIFIC OCEAN. CHRISTMAS ISLAND, Fosberg and Metraux 13237, 26 August, 1936 (UC 764241, f. *lata*). MARSHALL ISLANDS, Eniwetok Atoll, Taylor 46–424, 6 June, 1946 (MICH, *TYPE*); Rongelap Atoll, Taylor 46–506B, 21 June, 1946 (MICH); Bikini Atoll, Taylor 46–21, 15 March, 1946 (MICH); Bikini Atoll, Taylor 46–157, 3 April, 1946 (MICH, both as *H. gracilis* f. *lata*); Bikini Atoll, Taylor 46–82, 26 March, 1946 (MICH); Bikini Atoll, Taylor 46–189, 13 April, 1946 (MICH); Bikini Atoll, Taylor 46–222, 18 April, 1946 (MICH, the last three as *H. taenicola*); Bikini Atoll, Smith 47–32, July to August, 1947 (MICH); Bikini Atoll, Smith 47–182, July to August, 1947, (MICH, both as *H. taenicola*).

This species can be fairly readily distinguished from other Halimedae except possibly *H. cuneata*, by the frequent occurrence of subcuneate or obovate segments. The absence of a stalk or cushion segment separates it from this one species. Any confusion with *H. discoidea* or *H. taenicola* can be resolved microscopically by the absence of swollen secondary or tertiary utricles in *H. lacunalis*.

Histologically, the common occurrence of small secondary utricles is fairly characteristic of mature segments of this species, these being absent, however, when the cortex is composed of only two layers. In certain anatomical aspects *H. lacunalis* resembles *H. tuna*, particularly the Atlantic and Indian Ocean specimens. These similarities include the lateral attachment of the nodal fusion units, the regular surface appearance of the peripheral utricles, and the apparent absence of lateral fusions among them. In contrast, however, the diameters of the peripheral utricles are significantly smaller, with those of f. *lata* generally occurring towards the lower limit of the range. The adherence of the nodal groups is usually fairly considerable, the rigidity of the resulting nodal structure sometimes leading to confusion with the *H. incrassata* type of behavior. From this type of nodal union it is, nevertheless, entirely distinct, the units in *H. lacunalis* separating on teasing, since pores between adjacent nodal filaments are absent.

Halimeda gigas Taylor

Plate 1, Figure 3; Plate 5, Figure 15; Plate 6, Figure 5; Plate 9.

Halimeda gigas Taylor. 1950. p. 84, Plate 44, Figure 2.

Plants loosely organized, to 15 cm. tall; calcification rather light; color brownish-green, the surface slightly glossy, rugose, tending to crack somewhat on drying; branching complanate and sparse, although up to six segments may arise from a single one; basal segments subterete, the others plane, mainly discoidal to reniform, the outer margin entire or very slightly undulating, to 25 mm long, 42 mm broad and averaging 0.75–1.00 mm in thickness; shrinkage on drying fairly considerable, leaving a brown stain on paper.

Cortex of two, occasionally three layers of utricles; outermost utricles remaining attached after decalcification for an average distance of 8 microns, at times fusing laterally in twos and occasionally threes for this same distance; unfused peripheral utricles (96–)115–170 microns in surface diameter, 130–240 microns long in section, borne two or four on each secondary utricle; secondary utricles 60–120(–160) microns broad.

Nodal medullary filaments fusing in twos and threes for a length of several times the filament diameter, although occasionally and most particularly towards the periphery of the node uniting for only about one-quarter of this distance; fused groups entangled but at most adhering only slightly.

Type specimen: Marshall Islands, Eniwetok Atoll, Taylor 46–419, 6 June, 1946 (MICH).

Ecological and geographical distribution: Known only as dredged from 46 meters depth in the lagoon of the atoll; Marshall Islands in the North Pacific.

Specimen examined: PACIFIC OCEAN. MARSHALL ISLANDS, Eniwetok Atoll, Taylor 46–419, 6 June, 1946 (MICH, *TYPE*).

This species in external appearance and internal organization is a member of the *H. tuna* complex, seeming most closely related to the Pacific specimens of *H. tuna* with

large segments. It is readily distinguished, however, by the size of its segments which are the largest known for the genus. Also characteristic are the large surface diameters of the peripheral utricles, these averaging 140 microns in *H. gigas* as compared to 70 microns in *H. tuna*. In addition, the segment cortex is less extensively developed than in *H. tuna*. In the last two characteristics *H. gigas* resembles *H. macrophysa*. This latter species has peripheral utricles which are laterally free, and relatively small segments which are usually less than 15 mm long and 24 mm broad.

Halimeda macrophysa Askenasy

Plate 2, Figure 3; Plate 5, Figure 16; Plate 6, Figure 8; Plate 11.

Halimeda macrophysa Askenasy, 1888, p. 14, Plate 4, Figures 1–4; Barton, 1901, p. 17, Plate 2, Figures 15–18.

Plants fragile, compact and erect, arising from a single small holdfast region, to 10 cm tall; calcification moderate; color on drying whitish or pale greenish-white, the surface dull, rugose and appearing pitted; branching complanate, mainly ditrichotomous but with several segments arising from some of the larger ones; basal segments often subcuneate, the others friable, plane, commonly reniform or subreniform but also subcuneate, the upper margin entire, to 15 mm long, 24 mm broad and averaging 0.5 mm in thickness.

Cortex most commonly of two layers of utricles; outermost utricles separating readily on decalcification, appearing round in surface view, 135–180 microns in surface diameter, 170–230(–290) microns long, most commonly two but also one or four supported by each secondary utricle; secondary utricles 40–100 microns broad, 73–140 (–230) microns long.

Nodal medullary filaments fusing in twos, threes and occasionally larger units for a distance of several times the filament diameter; resultant units densely entangled and often adhering slightly.

Type locality: Matuku, Fiji Islands, South Pacific.

Ecological and geographical distribution: Collected in one to two meters of water and probably extending to greater depths; reported from the Fiji Islands (Askenasy, 1888) and the Tonga Islands (Barton, 1901) in the South Pacific, and in the North Pacific from the Marshall Islands (Dawson, 1957), the South Sea (Yamada, 1941), Borneo (Weber-van Bosse, 1913), and various locations in Melanesia including Timor (Barton, 1901).

Specimen examined: PACIFIC OCEAN. AUSTRALIA, Torres Strait, Murray Islands, Clark, October, 1913 (NY).

Few observations seem to have been recorded on the ecological distribution of this rather infrequently collected species, which in external appearance resembles members of the *H. tuna* complex. It is, however, readily distinguished from all species of the genus other than *H. javulosa* by its friable nature, and the pitted condition of the segment surface. The latter results from the extremely large peripheral utricles and their separation by calcium carbonate partitions, the green color of the utricles being somewhat masked as a result. From *H. javulosa* it can be separated macroscopically by its habit and segment morphology. Thus, reniform segments commonly occur in *H. macrophysa*, the plants themselves usually being compact and less than 10 cm tall, whereas in *H. javulosa* trilobed or cylindrical segments predominate, and the plants are attenuate

and to 22 cm in height. Anatomically, the cortex in both species is rather poorly developed, but the node structure is quite different, *H. macrophysa* belonging to the *H. tuna* complex, *H. javulosa* to the *H. incrassata* group.

Barton (1901) felt that *H. macrophysa* was closely allied to *H. tuna*, and maintained it as a separate taxon on the basis of the extremely large diameters of the peripheral utricles. Although these two species have common features, it would seem that *H. macrophysa* is not in the direct line of relationship. Instead, it differs from the large-segmented Pacific specimens of *H. tuna*, and from *H. gigas*, two taxa which have large peripheral utricles and which seem fairly closely related to *H. tuna*, in several characteristics. These include peripheral utricles which are separated by calcium carbonate partitions, the apparent absence or extremely limited occurrence of short fusion of the nodal filaments, and the rather undeveloped condition of the cortex.

Halimeda discoidea Decaisne

Plate 2, Figure 5; Plate 5, Figure 11; Plate 6, Figure 11; Plate 7, Figures 9–10; Plate 8, Figures 5–8; Plate 11.

Halimeda discoidea Decaisne, 1842, p. 91; Kützing, 1849, p. 504; De Toni, 1889, p. 527; Collins, 1909–18, p. 400; Howe, 1907, p. 495, Plate 25, Figures 11–20, Plate 26; Setchell and Gardner, 1920, p. 177, Plate 13, Figure 3; Taylor, 1928, p. 82, Plate 10, Figure 17, Plate 11, Figure 23; Taylor, 1950, p. 85, Plate 45, Figures 1–2; Egerod, 1952, p. 398, Plate 38, Figures 19 b–d.

Halimeda discoidea v. *platyloba* Børgesen, 1911, p. 134, Figure 3; Børgesen, 1913, p. 107, Figure 86.

Halimeda discoidea f. *intermedia* Gilbert, 1947, p. 126.

Halimeda discoidea f. *subdigitata* Gilbert, 1947, p. 125.

Halimeda tuna Barton, 1901, p. 11 in part.

?*Halimeda cuneata* f. *digitata* Barton, 1901, p. 16, Plate 2, Figure 9.

Plants generally compact, forming cushion-like clumps, but occasionally loose, arising from a small but distinct holdfast region, to 18 cm tall; calcification light; color on drying creamish-white to green or sometimes brown, the surface dull or somewhat glossy; branching mainly ditrichotomous but polychotomous from large segments; the basal first to second segments subcylindrical or broadly cuneate and often of a substipitate nature; other segments usually plane, commonly discoidal to reniform but also compressed-cylindrical, cuneate or subcuneate, the outer margin entire, undulating or somewhat deeply cleft, the latter possibly resulting from environmental influences, to 29 mm long, 33 mm broad and averaging 0.75–1.25 mm in thickness.

Cortex of two, occasionally three layers of utricles; outermost utricles remaining firmly attached after decalcification for an average distance of 42 microns, often fusing laterally in twos, threes and occasionally fours for this same distance, unfused peripheral utricles (30–)40–90 microns in surface diameter, 45–120(–210) microns long in section, up to 14 being supported by each secondary utricle; innermost utricles somewhat contiguous at their apical end, or when well-developed for most of their length, (70–)95–155(–260) microns broad, 100–350(–435) microns long.

Nodal medullary filaments united in twos and threes, the length of fusion usually

1.5 or several times the filament diameter; fused units entangled but at most adhering only slightly.

Type specimen: In the Muséum National d'Histoire Naturelle, Paris; the label, as observed in a photograph of this specimen taken by Professor Taylor, indicates that the plant was collected at Kamtschatka during a voyage of the *Venus*; at least the locality probably in error.

Ecological and geographical distribution: From below low-tide line to at least 50 meters depth; frequently attached to rocks but also growing on sand flats; pantropical.

Representative specimens examined: NORTH ATLANTIC. COLOMBIA, Bahia Honda, Taylor 39–287, 3 April, 1939 (MICH). PANAMA, Caledonia Bay, Taylor 39–216, 3 April, 1939 (MICH). MARTINIQUE, Hamel 103, 21 March, 1930 (MICH, NY). GUADELOUPE, Feldmann 3493, 25 March, 1936 (MICH); Questel 246, March, 1944 (WRT). VIRGIN ISLANDS, Børgesen 1872, 1905–06 (NY). PUERTO RICO, Britton, Brown and Cowell, 25 February, 1915 (NY, fruiting slightly); Howe 1823, 15 May, 1905 (NY). JAMAICA, Taylor 56–297b, 30 March, 1956 (WRT). CUBA, Henderson and Bartsch 73c, 14 May, 1914 (NY). BAHAMAS, Howe 3674, 5 February, 1905 (NY). FLORIDA, Dry Tortugas, Taylor 411, 23 July, 1924 (NY); Caesar's Creek, south of Elliott's Key, Howe 2964, 31 March, 1904 (NY). CAPE VERDE ISLANDS, Moseley, August, 1873 (BM); Welwitsch 247, August, 1853 (BM, both as *H. tuna*).

SOUTH ATLANTIC: BRAZIL, south of Recife, Williams, February, 1945 (DUKE); Barro Grande, Moseley, September, 1873 (BM, as *H. tuna*).

NORTH PACIFIC: REVILLA GIGEDO ISLANDS, Taylor 34–54, 5 January, 1934 (MICH). MARIA MAGDALENA ISLAND, Taylor 39–657, 9 May, 1939 (MICH). MEXICO, Baja California, Vives 4, 28 February, 1911 (NY); Guaymas, Marchant 105 (NY). COSTA RICA, Golfo Dulce, Taylor 39–36, 26 March, 1939 (MICH). HAWAIIAN ISLANDS, Reed 569 (NY, fertile); Rogers, 31 May, 1946 (NY); Heller 2234, 26 April, 1895 (BM, NY); Home (BM, as *H. tuna* ad f. *albertisii*); Tilden 451, 18 May, 1900 (BM, NY, as *H. tuna*). MIDWAY ISLANDS, Pearl and Hermes Reef, Galstoff, 26 July, 1930 (NY, as *H. cuneata*). MARSHALL ISLANDS, Bikini Atoll, Taylor 46–86, 29 March, 1946 (MICH). JAPAN, Shima, Higashi, August, 1923 (UC 315236, as *H. cuneata*). FORMOSA, Yamada, April, 1941 (UC 958454, as *H. cuneata*). PHILIPPINES, Babuyan Islands, Bartlett 14618, 17 July, 1935 (MICH); Merrill 9147, April, 1913 (NY, as *H. cuneata*). MALAYA, Singapore, Anon., *ex* herb. Hauck and Collins (NY, as *H. cuneata*). SUMATRA, Kostermans 729, 19 October, 1938 (MICH). JAVA, Kostermans 271, 4 October, 1938 (MICH). FAN, Siboga Expedition (NY, as *H. cuneata* f. *versatilis*). LESSER SUNDA ISLANDS, Setchell and Setchell BS 145, 15 June, 1929 (UC 624477).

SOUTH PACIFIC. SOCIETY ISLANDS, Lesson, 1825 (NY, as *H. lessonii*); Setchell and Parks 5008, 19 May, 1922 (NY); Seurat, 20 January, 1903 (BM, as *H. tuna*). COOK ISLANDS, Parks 22318, 1929 (UC 633580). NEW HEBRIDES, Anon., *ex* herb. Merrifield (BM, as *H. macroloba*). AUSTRALIA, Queensland, Bailey (BM); Tully (BM, both as *H. cuneata*).

INDIAN OCEAN. AMIRANTE ISLAND, Gardiner (BM, as *H. tuna*). SOMALILAND, Hildebrandt 821, March, 1873 (UC 434121, as *H. tuna*). SUDAN, Harvey-Gibson (BM, as *H. cuneata*). RED SEA, Boissier (NY, as *H. macroloba*). ARABIA, Lunt, 1893–94 (BM, as *H. papyracea* and *H. cuneata*). NICOBAR ISLANDS, Mora-

vian Missionaries (BM, as *H. cuneata* f. *digitata*). CEYLON, Ferguson 67 (BM); Harvey 70 (BM, both as *H. tuna*). MAURITIUS ISLAND, Robillard, 1881 (BM, as *H. tuna*).

The epithet *discoidea* was first applied by Esper (1798–1806, Plate 11) to a drawing of Halimeda labelled *Corallina discoidea.* This plant, apparently Mediterranean, was later placed in synonymy under *H. tuna* by Hammer in his continuation of Esper's work (1830). Even were this relationship not accepted, Esper does not qualify as author of *H. discoidea,* since a plate unaccompanied by analysis of parts does not constitute valid publication (Lanjouw, 1956). The plant was later described by Decaisne (1842).

This species, although frequently mistaken for *H. tuna* and *H. cuneata,* is microscopically quite distinct, and is characterized in particular by the swollen utricles of the inner cortex, one layer being the most common. When an additional zone is present, it rarely occurs uniformly throughout the segment, the innermost utricles in such cases often tending towards the lower limit of the size range. Relatively small secondary utricles often occur in Pacific-Mexican plants, and in some of the Hawaiian Halimedae. This irregularity was also noted by Howe (1911).

Subsequent to the removal, by Howe (1907), of this species from synonymy under *H. tuna* where it had been relegated by Barton (1901), three subspecific taxa have been described: v. *platyloba* (Børgesen, 1911) from deep water, f. *subdigitata* (Gilbert, 1947) including plants which resemble *H. cuneata,* and f. *intermedia* (Gilbert, 1947) of specimens intermediate between f. *discoidea* and f. *subdigitata.* Consistent with the treatment accorded entities based mainly on modifications of habit or segment morphology which seem unaccompanied by significant histological differences, these three taxa, all representing changes of approximately the same degree rather than at the two levels of variety and form, have not been given separate taxonomic standing.

Halimeda taenicola Taylor

Plate 2, Figure 6; Plate 5, Figure 12; Plate 6, Figure 14; Plate 11.

Halimeda taenicola Taylor, 1950, p. 86, Plate 46, Figure 1.

Plants erect and compact, arising from a small holdfast region, to 15 cm tall; calcification moderate; color on drying golden, cream, white, or in the younger regions occasionally greenish, the surface generally glossy and smooth but sometimes rugose; branches numerous with up to five arising from a single segment; the lowermost one to two segments usually compressed-cylindrical to subcuneate and often of a substipitate nature; others plane, often becoming concave on drying, generally subcuneate to trapezoidal, less commonly subcylindrical or reniform, the upper margin entire, to 11 mm long, 18 mm broad, and averaging 1.0–1.5 mm in thickness.

Cortex of two to three layers of utricles; innermost utricles remaining firmly attached after decalcification for an average distance of 19 microns, sometimes fusing laterally in twos and threes for this same distance, unfused peripheral utricles (20–)40–75(–86) microns in surface diameter, (45–)56–125(–140) microns long in section, their lateral and peripheral margins sometimes thickened, four or occasionally up to six supported by each secondary utricle; if three layers of utricles present the secondary ones relatively small, 26–60(–80) microns broad, (30–)40–90 microns long; innermost utricles usually rather large, 75–160(–190) microns broad.

Nodal medullary filaments generally uniting in twos and threes for a distance of several times the filament diameter; fused units entangled and adhering laterally for 40–70 microns.

Type specimen: Marshall Islands, Rongerik Atoll, Enyvertok Island, Taylor 46–551, 29 June, 1946 (MICH).

Ecological and geographical distribution: Usually growing in rather shallow water where the plants may become exposed at low-tide, also dredged from 37 meters depth; known for the North Pacific Ocean.

Representative specimens examined: PACIFIC OCEAN. PALMYRA ISLAND, Rock, summer, 1913 (NY, as *H. macroloba*). GILBERT ISLANDS, Onotoa, Moul 8116, 9 July, 1951 (WRT). Onotoa, Moul 8270, 4 August, 1951 (WRT); Onotoa, Moul 8434, 22 August, 1951 (WRT). MARSHALL ISLANDS, Bikini Atoll, Taylor 46–45, 18 March, 1946 (MICH); Bikini Atoll, Taylor 46–149, 3 April, 1946 (MICH); Bikini Atoll, Taylor 46–228, 16 April, 1946 (MICH); Rongelap Atoll, Taylor 46–456A, 21 June, 1946 (MICH); Rongelap Atoll, Taylor 46–593, 16 July, 1946 (MICH); Rongelap Atoll, Taylor 46–622, 27 July, 1946 (MICH); Rongerik Atoll, Taylor 46–523, 27 June, 1946 (MICH); Rongerik Atoll, Taylor 46–551, 29 June, 1946 (MICH, *TYPE*).

In general form *H. taenicola* frequently appears like a Caribbean *H. discoidea* with thick segments, but may often be distinguished macroscopically by the concave appearance of the segments on drying, and the somewhat heavier degree of calcification, the color being usually white or creamish. Its internal structure also shows resemblances to *H. discoidea*, and the rather characteristically expanded utricles of the innermost, usually tertiary layer of the cortex, although somewhat smaller in average diameter, are reminiscent of the secondary utricles of this other species. In *H. taenicola* these utricles often support five or six relatively small secondary ones, as opposed to only four or two which are the more usual numbers for most species with a three-layered cortex. On occasion this intermediate zone may be absent, but such rarely happens uniformly throughout the segment. In the more basal segments an additional layer is frequently present, the length of the peripheral and secondary utricles is often greater, and the breadth of the innermost utricles is towards the lower limit of the range. Such modifications occur fairly commonly throughout the genus, and have been discussed in the section on morphology and anatomy. They cannot, however, be ignored when identifying specimens since the diagnostic characteristics of a species are frequently somewhat masked if such segments are selected.

Histologically, this species differs from *H. discoidea* in the somewhat smaller surface diameters of the peripheral utricles, these averaging 57 microns in *H. taenicola* and 65 microns in *H. discoidea*. Other differences include the relatively fewer lateral fusions of these utricles, and the degree of their lateral attachment, which in *H. taenicola* is approximately half that occurring in *H. discoidea*. Although the basic nodal structure is similar in these two species, short fusion is considerably more common in *H. discoidea* with the fusion groups at most adhering only slightly. In *H. taenicola* these units are attached laterally for an appreciable distance.

The external appearance of this species sometimes leads to confusion with *H. macroloba*. A separation can usually be made macroscopically on the basis of the rather extensive holdfast region, and the somewhat fused condition of the basal or suprabasal segments which commonly occur in *H. macroloba* but which are absent in *H. taenicola*. Histologically, the two species are entirely distinct. The peripheral utricles in *H. macro-*

loba separate after decalcification, and the behavior of its nodal filaments is of the *H. incrassata* type.

Halimeda gracilis Harvey *ex* J. Agardh

Plate 2, Figure 4; Plate 5, Figure 7; Plate 6, Figure 9; Plate 7, Figure 2; Plate 10.

Halimeda gracilis Harvey *ex* J. Agardh, 1887, p. 82; Harvey's Ceylon Algae no. 72; Barton, 1901, p. 22, Plate 3, Figures 28–32; Collins, 1909–18, p. 399.

Halimeda gracilis v. *opuntioides* Børgesen, 1911, p. 144, Figure 11; Børgesen, 1913. p. 108, Figure 87.

?*Halimeda gracilis* f. *laxa* (Barton) Barton, 1901, p. 22, Plate 3, Figure 29; *Halimeda laxa* Barton, 1900, p. 479, Plate 18, Figure 1–3.

?*Halimeda gracilis* f. *elegans* Yamada, 1941, p. 20, Figure p. 21; Yamada, 1944a, p. 28, Plate 3.

Halimeda cuneata Kützing, 1857, p. 8, Plate 21, Figure 3.

Plants flaccid, straggling and decumbent, to over 40 cm long, calcification moderate to heavy; color on drying white or greenish; the surface usually glossy; branching sometimes sparse but usually frequent with up to five branches arising from a single segment; segments ribbed, chalky to brittle, at times subcylindrical but more commonly subcuneate to reniform, the upper margin entire, undulate, or lobed, to 9 mm long, 15 mm broad, and averaging 0.50–0.75 mm in thickness.

Cortex of two, sometimes three layers of utricles, these generally produced by dichotomies in the lateral branches of the medullary filaments; outermost utricles usually remaining slightly attached on decalcification, occasionally separating but still appearing hexagonal rather than rounded in surface view, 23–58(–70) microns in surface diameter, 40–90(–110) microns long in section, up to eight supported by each secondary utricle; secondary utricles clavate, 23–70(–125) microns broad, usually relatively long and frequently extending to the medulla.

Nodal medullary filaments fused most commonly in twos but occasionally in threes for a distance of several times the filament diameter; the resultant groups not entangled and at most adhering only slightly.

Type specimen: Harvey's Ceylon Algae no. 72; isotype material in several herbaria, including the British Museum and the New York Botanical Garden.

Ecological and geographical distribution: Known only from deep water having been collected from approximately 10 meters to somewhat over 60 meters depth; pantropical.

Representative specimens examined: ATLANTIC OCEAN. VIRGIN ISLANDS, Børgesen 2197, 27 March, 1906 (NY); Moseley (BM). PUERTO RICO, Howe 7153, 25 June, 1915 (NY); Howe 7156a, 25 June, 1915 (NY); Howe 7369, 4 July, 1915 (NY); Howe 7618, 10 July, 1915 (NY). JAMAICA, Taylor 56–296, 30 March, 1956 (WRT).

PACIFIC OCEAN. HAWAIIAN ISLANDS, Setchell and Setchell 10345, 12 July, 1924 (UC 622514). TORRES STRAIT, Moseley (BM, as *H. cuneata*).

INDIAN OCEAN. AMIRANTE ISLAND, Gardiner, 9 October, 1905 (BM); Gardiner, 11 October, 1905 (BM). SAYA DE MALHA, Gardiner (BM, UC 435470). PAMOAN and KRUSADAI ISLANDS, Swamy, December to January, 1941–1942 (UC 736701). CEYLON, Harvey 72 (BM, NY, *ISOTYPE* material).

This species seems closely related to *H. lacrimosa* and probably also to *H. bikinensis*. From the latter taxon which consists of relatively compact specimens with large segments, to 16 mm long and 25 mm broad, *H. gracilis* is readily distinguished by its loose straggling habit, reaching a length of over 40 cm, and its smaller segments, to 9 mm long and 15 mm broad. In contrast, plants of *H. lacrimosa* rarely exceed 5 cm in length, and are composed largely of spherical or tear-shaped segments rather than flat ones.

Although *H. gracilis* is pantropical, its known distribution is extremely limited as compared to that of *H. discoidea* or *H. opuntia*. The paucity of records can be at least partly attributed to the fewer collections of deep-water plants, and to the relatively frequent misidentifications of this species as *H. opuntia*, and less commonly as *H. incrassata* or *H. tuna*. Cases which are doubtful macroscopically can be fairly readily resolved by a study of histological characteristics including nodal medullary filament behavior and the appearance of the cortical layers. These are both quite distinctive for *H. gracilis*.

The peripheral utricles in plants of this species may at first appear rounded in surface view, and thus give the impression of being separate. A more careful examination, however, usually reveals that they are at least slightly attached, though often by only the thin platform-like extensions of the outer surface. The different optical properties of these edges, and the slightly convex outer face of the utricles combine to produce the illusion of roundness. These edges in addition, may sometimes create the impression of a matrix surrounding the utricles. This may represent the condition described by Barton for some of these plants.

Four infraspecific categories have been designated for this species: *v. opuntioides* (Børgesen, 1911), f. *laxa* (Barton, 1901), f. *elegans* (Yamada, 1941), and f. *lata* (Taylor, 1950), the latter having been transferred to *H. lacunalis*. The modifications described for f. *elegans*, that of ribbed segments, and for f. *laxa*, peripheral utricles imbedded in a non-calcareous matrix, occur in typical plants, whereas the somewhat more lax habit of this second form and the larger segments of v. *opuntioides* are in all probability environmental responses. Since these three entities do not seem significantly different to merit separate rank they have been placed in synonymy under *H. gracilis*.

Halimeda lacrimosa Howe

Plate 2, Figure 2; Plate 5, Figure 8; Plate 6, Figure 12; Plate 7, Figures 4–6; Plate 10.

Halimeda lacrimosa Howe, 1909, p. 93, Plate 4, Figure 1; Plate 6, Figures 3–11; Collins, 1909–18, p. 399.

Plants fragile, straggling and decumbent, to 5 cm long; calcification heavy; color on drying white, often becoming bluish-green towards the apex, the surface smooth and usually glossy; branching restricted, generally ditrichotomous; segments easily crushed on drying, the basal ones usually cylindrical, often moniloid; others and particularly the more apical ones commonly spherical or "tear"-shaped, to 5 mm in the three dimensions.

Cortex of two to three layers of utricles, these often produced by dichotomies or tetrachotomies in the lateral branches of the medullary filaments; outermost utricles usually remaining slightly attached on decalcification, occasionally separating but still appearing hexagonal rather than rounded in surface view, 31–42 microns in surface diameter, 40–110 microns long in section, generally 6–18 supported by each secondary

utricle; secondary utricles capitate, 66–110 microns broad at the apical end, 105–340 (–400) microns long.

Nodal medullary filaments uniting in twos, threes, and fours for approximately 1.5 or several times the filament diameter, short and extended fusions often mixed so that fewer filaments may emerge than participate in the fusion; resultant units not particularly entangled and at most adhering only slightly.

Type specimen: Bahamas, Mariguana, Howe 5524, 11 December, 1907 (NY).

Ecological and geographical distribution: Extending from near low-tide level to at least 20 meters depth; collected on stones, in sand, and on the stipes of *Avrainvillea*; of apparently restricted distribution within the Caribbean.

Specimens examined: ATLANTIC OCEAN. CUBA, Henderson and Bartsch 306d, 24 May, 1914 (NY). BAHAMAS. Howe 5492, 10 December, 1907 (NY); Howe 5504, 11 December, 1907 (NY); Howe 5524, 11 December, 1907 (NY, *TYPE*); Howe 5810, 24 December, 1907 (NY).

This delicate species is readily distinguished from other members of the genus by its small size and by the fairly common occurrence of spherical or pyriform segments. It shares with *H. gracilis*, probably the most closely related species, several features including a lax decumbent habit, and an essentially dichotomous inner cortex. The general appearance and degree of attachment of the peripheral utricles are also common to the two species and have been discussed in the taxonomic treatment of *H. gracilis*.

Histologically, *H. lacrimosa* is characterized by capitate secondary utricles which appear circular in cross-section and support up to 18 peripheral utricles. The behavior of the nodal medullary filaments is rather complex, it perhaps best being interpreted as a combination of short and extended fusion with for example, two filaments resulting from a fusion of three or four (Plate 7, Figures 5, 6). The usual type of extended fusion also occurs.

The restricted distribution of this species may be partly accounted for by the ease with which such small specimens are overlooked. Also, these plants commonly occur in relatively deep water where it is more difficult to make representative collections.

Halimeda bikinensis Taylor

Plate 2, Figure 1; Plate 5, Figures 17–18; Plate 6, Figure 3; Plate 10.

Halimeda bikinensis Taylor, 1950, p. 87, Plate 48, Figure 1.

Plants erect, moderately compact or somewhat loose, arising from a small holdfast region, to 20 cm tall; calcification relatively heavy; color on drying grayish to white or cream, the surface dull and rugose; branching somewhat sparse with up to four or five segments and occasionally more arising from a single one; basal segments subcylindrical, subcuneate to subreniform, the three to four lowermost ones often devoid of branches; the others brittle, sometimes discoid but more commonly subreniform to reniform with subcuneate segments frequently occurring at the bases of the branches, the outer margin entire or slightly undulating, frequently raised and infolded, measuring to 16 mm long, 25 mm broad, and averaging 0.7–1.0 mm in thickness.

Cortex of two to three layers of utricles produced by dichotomies in the lateral branches of the medullary filaments; the outermost utricles remaining slightly attached or separating on decalcification, appearing rounded in surface view, 23–47 microns in surface diameter, (48–)60–105(–125) microns long in section, most commonly four

but up to eight borne on each secondary utricle; secondary utricles usually not constricted at their origin, 20–47 microns broad.

Nodal medullary filaments occasionally remaining separate but more commonly uniting in twos and threes, the length of fusion usually 1.5 or several times the filament diameter; the resultant units not particularly entangled, and at most adhering only slightly.

Type specimen: Marshall Islands, Namu Islands, Bikini Atoll, Taylor 46–156, 3 April, 1946 (MICH).

Ecological and geographical distribution: Collected in moderately deep water in the North Pacific, and to over 80 meters depth in the Indian Ocean.

Specimens examined: PACIFIC OCEAN. GILBERT ISLANDS, Onotoa, Moul 8467, 25 August, 1951 (WRT). MARSHALL ISLANDS, Bikini Atoll, Taylor 46–43, 18 March, 1946 (MICH); Bikini Atoll, Taylor 46–156, 3 April, 1946 (MICH, *TYPE*); Bikini Atoll, Taylor 46–190, 13 April, 1946 (MICH); Bikini Atoll, Taylor 46–193C, 13 April, 1946 (MICH, both as *H. tuna*). LESSER SUNDA ISLANDS, South Bali, Pullai BK 376, June, 1933 (UC 624497, as *H. opuntia*).

INDIAN OCEAN. CARGADOS CARAJOS, Gardiner (BM, from 30 fathoms and 47 fathoms, both as *H. tuna* f. *platydisca*). SAYA DE MALHA, Gardiner (BM, as *H. tuna* f. *platydisca*).

In external appearance this species is most commonly confused with specimens of *H. tuna* with large segments, with *H. discoidea*, and to a lesser extent with *H. gigas*. A number of well-defined distinctions exist for *H. bikinensis*, however, including the greater degree of calcification of its segments, the dichotomous nature of the inner cortex, the smaller surface diameters of the peripheral utricles, and the relative ease of separation of these utricles. This last characteristic, which varies somewhat with age, is discussed in greater detail in the section on morphology and anatomy.

Histologically, this species appears to have most in common with *H. gracilis* and *H. lacrimosa*. Characteristic of these two species and most particularly the latter are the somewhat swollen apical ends of the secondary utricles which in turn support several, usually 6–18 peripheral utricles. Such, however, are absent in *H. bikinensis*, although the appearance is somewhat simulated by some of the broader secondary utricles which may bear up to eight peripheral utricles rather than the more usual two or four.

Halimeda opuntia (Linnaeus) Lamouroux

Plate 2, Figures 7–8; Plate 5, Figures 3–4; Plate 6, Figure 6; Plate 7, Figure 3; Plate 10.

Corallina opuntia Linnaeus, 1758, p. 805 *p.p.*

Halimedea opuntia Lamouroux, 1812, p. 186; *Halimeda opuntia*, Barton, 1901, p. 18, Plate 2, Figures 19–27; Collins, 1909–18, p. 400, Plate 17, Figure 156; Taylor, 1928, p. 82, Taylor, 1950, p. 80, Plate 39, Figure 1; Egerod, 1952, p. 397, Plate 37, Figure 19a, e, and f.

Halimeda multicaulis (Lamarck) Lamouroux, 1816, p. 307. *Flabellaria multicaulis* Lamarck, 1813, p. 302.

Plants compact or somewhat loose in organization, often with both axial and lateral systems of growth holdfast region not restricted to the initial area but diffuse, with

patches of rhizoids occurring at intervals where the plant comes in contact with the substratum, to over 30 cm long; calcification moderate to heavy; color on drying golden, cream, white or greenish, the surface dull or glossy; branches sometimes few but often numerous, arising in more than one plane from successive segments; segments extremely variable, flat or somewhat contorted and frequently ribbed, cylindrical or oblong to auriculate, the upper margin entire, undulate or lobed, to 12 mm long, 20 mm broad, and averaging 0.3–0.5 mm in thickness.

Cortex of up to five zones of utricles formed by dichotomies in the lateral branches of the medullary filaments; outermost utricles adhering slightly after decalcification or for as much as 6 microns, appearing somewhat rounded or hexagonal in surface view, 12–63 microns in surface diameter, 15–70 microns long in section; secondary utricles 11–50 microns broad.

Nodal medullary filaments uniting most commonly in pairs for a distance of approximately 1.5 times the filament diameter, occasionally fusing in threes but rarely in fours, seldom remaining separate; adjacent fused units free or laterally attached for up to 25 microns.

The following two varieties of this species have been recognized.

Halimeda opuntia (Linnaeus) Lamouroux v. *opuntia*

Halimeda opuntia f. *typica* Barton, 1901, p. 20, Plate 2, Figure 19; Taylor, 1928, p. 83, Plate 10, Figures 5–7; Plate 11, Figure 17.

Halimeda opuntia f. *cordata* (J. Agardh) Barton, 1901, p. 20, Plate 2, Figure 21. *Halimeda cordata* J. Agardh, 1887, p. 83.

Halimeda opuntia f. *elongata* (Barton) Barton, 1901, p. 21, Plate 2, Figure 24; Taylor, 1950, p. 82, Plate 41. *Halimeda cuneata* v. *elongata* Barton, 1900, p. 480, Plate 18, Figures 4–5.

Halimeda opuntia f. *intermedia* Yamada, 1934, p. 81, Figures 50–51.

Halimeda opuntia f. *minima* Taylor, 1950, p. 82, Plate 39, Figure 2.

Halimeda opuntia f. *minor* Vickers, 1905, p. 57; Taylor, 1928, p. 83, Plate 10, Figures 3–4.

Halimeda opuntia f. *renschii* (Hauck) Barton, 1901, p. 21, Plate 2, Figures 22, 22a. *Halimeda renschii* Hauck, 1886, p. 167.

Halimeda opuntia f. *triloba* (Decaisne) Barton, 1901, p. 20, Plate 2, Figure 20; Taylor, 1928, p. 83, Plate 10, Figure 2; Taylor, 1950, p. 81, Plate 40, Figure 2. *Halimeda triloba* Decaisne, 1842, p. 102.

Segment shape variable, cylindrical or oblong to auriculate, the upper margin entire, undulate or lobed, to 7 mm long, 11 mm broad, with an occasional larger segment sometimes occurring; peripheral utricles 12–41 microns in surface diameter, 15–39(–50) microns long in section; secondary utricles 11–35 microns in width.

Halimeda opuntia v. *hederacea* (Barton) **n. comb.**

Halimeda opuntia f. *hederacea* Barton, 1901, p. 21, Plate 2, Figure 23; Taylor, 1950, p. 81, Plate 40, Figure 1.

Halimeda opuntia forma Taylor, 1950, p. 83.

?*Halimeda incrassata* f. *distorta* Yamada, 1941, p. 119, Figure p. 120; Yamada, 1944a, p. 28, Plate 4.

Predominating segment shapes in the non-rhizomatous portion of the plant truncate-reniform to auriculate, upper margin entire to shallowly lobed, occasionally deeply in-

dented, relatively large, to 12 mm long, 20 mm broad; peripheral utricles 25–63 microns in surface diameter, 28–70 microns long in section; secondary utricles 15–52 microns in width.

Type localities: Jamaica for the v. *opuntia;* the v. *hederacea* was described from a specimen collected on the Siboga Expedition to Indonesia.

Ecological and geographical distribution: From low-tide level to 80 meters depth; found on rocks, gravel and sand, often forming extensive mats; the v. *opuntia* is pantropical, whereas v. *hederacea* is known only from the Pacific.

Representative specimens examined: ATLANTIC OCEAN. VENEZUELA, Margarita Island, Blakeslee (UC 470356); Tortuga Island, Taylor 39–560a, 21 April, 1939 (MICH). NETHERLANDS ANTILLES, Curacao Island, Taylor 39–569, 23 April, 1939 (MICH); Aruba Island, Taylor 39–324, 10 April, 1939 (MICH). PANAMA, Caledonia Harbor, Taylor 39–159, 3 April, 1939 (MICH). COSTA RICA, Portetti near Limon, Stork, 15–20 July, 1932 (MICH, UC 696506). SAN ANDRES ISLAND, Proctor, 22–27 April, 1948 (MICH). PROVIDENCIA ISLAND, Proctor 3463, 29 April to 9 May, 1948 (MICH). BRITISH HONDURAS, Schipp A 110, 8 May, 1933 (MICH). MEXICO, Vera Cruz, Hildebrand, 19 April, 1956 (DUKE). TRINIDAD, Bronniman, 1949 (WRT). TOBAGO, Taylor 39–512, 20 April, 1939 (WRT). BARBADOS, Vickers 44, 17 March, 1903 (BM). MARTINIQUE, Hamel and Hamel 129, 23 March, 1930 (MICH). GUADELOUPE, Mazé, 1894 (WRT). DESIRADE, Feldmann 3492, 25 March, 1936 (MICH). ST. BARTHELEMY, Questel 402, 29 June, 1938 (MICH, as *H. simulans*). VIRGIN ISLANDS, Børgesen, 1905–06 (MICH). PUERTO RICO, Chardon and Otero 1, 25 May, 1944 (WRT). HISPANIOLA, Haiti, Bartlett 17983, 23 June, 1941 (WRT). JAMAICA, Lewis A528, 19 June, 1949 (MICH). CUBA, Proctor 3152, 4–9 April, 1948 (MICH). BAHAMAS, Wilson 8069, 15–18 May, 1909 (WRT). FLORIDA, Taylor 29, 9 June, 1924 (WRT).

NORTH PACIFIC OCEAN. GUADALUPE ISLAND, Mason 28 (UC 363283, v. *hederacea*). REVILLA GIGEDO ISLANDS, Taylor 39–24a, 16 March, 1939 (MICH). HAWAIIAN ISLANDS, Eubank 647, 13 April, 1947 (UC 928271, v. *hederacea*). PALMYRA ISLAND, Rock (UC 294567). GILBERT ISLANDS, Moul and Cloud 8256B, 27 July, 1951 (WRT, v. *hederacea*); Moul, Cloud and Strasburg 8318, 9 August, 1951 (WRT). MARSHALL ISLANDS, Bikini Atoll, Taylor 46–12, 11 March, 1946 (MICH); Bikini Atoll, Smith 47–159, July to August, 1947 (MICH, v. *hederacea*). MARIANA ISLANDS, Moran, 4 August, 1954 (UC M 021615). RYUKYU ISLANDS, Yamada (UC 531861). FORMOSA, Fan 1071, 25 April, 1951 (UC 936280). PHILIPPINES, Sulu Archipelago, Bartlett 16035, 15 September, 1935 (MICH, fertile); Luzon, Santos 118, 14 July, 1935 (MICH, fertile, as *H. gracilis*); Zamboanga, Balhani 256, January to February, 1941 (MICH, v. *hederacea*). MALAYA, Teysmann (MICH, UC 953410). SUMATRA, Kostermans 731b, 19 October, 1938 (MICH). JAVA, Setchell JP 546, May, 1929 (UC 624502). LESSER SUNDA ISLANDS, Bali, Pullai 382, July, 1933 (UC 624482). BORNEO, Kjellmann, September, 1879 (UC 431044). CELEBES, Palm (MICH). MOLUCCAS, Robinson 2394, July to November, 1913 (UC 203417).

SOUTH PACIFIC OCEAN. EASTER ISLAND, Crocker 9821, 15 January, 1934 (UC 633788). GAMBIER ISLAND, Crocker 9813, 1934 (UC 633804). TUBUAI ISLANDS, Rurutu Island, Crocker 9806, 26 November, 1934 (UC 633728). SOCIETY ISLANDS, Crossland 6661 in part, May, 1925 (UC 667812). COOK ISLANDS, Parks 7, 1929 (UC 633579). TONGA ISLANDS, Parks 17611, 1926 (UC 667591). SAMOA

ISLANDS, Crocker 2, 14 October, 1936 (UC 633960). FIJI ISLANDS, Parks 17812, summer, 1927 (UC 667519). SOLOMON ISLANDS, Crocker 0631D, 16 May, 1933 (UC 513220). NEW GUINEA, Kärubach, 28 June, 1888 (UC 409051). TORRES STRAIT, Murray Islands, Clark, October, 1913, (UC 470333, v. *hederacea*).

INDIAN OCEAN. RED SEA, opposite Kosseir, Schimper 932, 1837 (UC 436441, as *H. multicaulis*). SAYA DE MALHA, Gardiner (BM, UC 435469). MAURITIUS ISLAND, Anon. (MICH). MADAGASCAR, Hariot, July, 1901 (BM, as *H. incrassata* f. *ovata*). COMORO ISLAND, Hildebrandt 1889, August, 1889 (UC 434121).

A complete list of the early synonymy for the species is given by Barton (1901, p. 18); additional illustrative material is contained in the following: Ellis and Solander, 1786, Plate 20, Figure b, as *Corallina opuntia;* Lamouroux, 1821, Plate 20, Figure b (figure taken from Ellis and Solander); Kützing, 1843, Plate 43, Figure 2; Kützing, 1857, Plate 21, Figures 1–2 (Figure 2 as *H. multicaulis*); Harvey, 1858, Plate 11, Figure b; Zanardini, 1858, Plate 2.

Members of this species are readily distinguished macroscopically by the existence of several points for attachment to the substrate and the common occurrence of branching in more than one plane. Microscopically, the extremely small peripheral utricles and the short fusion in pairs of the nodal filaments are very characteristic. Special morphological features include the occasional termination of a branch with rhizoidal rope-like strands rather than segments, and the development in certain specimens of two fairly dissimilar growth systems (Plate 2, Figure 7). Of these, the axial one, which is somewhat loosely organized and composed of cylindrical and deeply trilobed segments or occasionally subcuneate ones, gives rise to lateral systems. These latter consist of numerous compactly branched units in which flat, relatively broad segments with entire or slightly lobed margins are often the most common.

The morphology of the segments is extremely variable, and as a result, plants with a predominating type of segment were frequently designated as distinct species by the workers of the nineteenth century. Barton (1901) lowered three of these to the rank of forms within *H. opuntia,* and indicated three additional forms. Three new forms have since been described. The study of these various entities revealed several limitations, including the difficulty of correct assignment of unidentified material. As might be expected, some specimens do not correspond to any of the described infraspecific groups, whereas others seem to fall into at least two different categories as, for example, the plant with the axial system just described (Plate 2, Figure 7). It approaches both f. *elongata* and f. *typica* of Barton's classification, which suggests the possibility of different portions of the same plant, particularly as obtained from dredge hauls, being delimited as separate entities.

The results of a comparative examination of these forms indicated a separation into two fairly distinct categories within *H. opuntia* on the bases of segment size, and surface diameters of the peripheral utricles. The majority of the forms, including f. *typica,* fall into the first category which has been named v. *opuntia.* These plants possess relatively small segments and their peripheral utricles average 27 microns in surface diameter. The second category is composed of specimens with large segments, the diameters of their peripheral utricles averaging 44 microns. Members of Barton's f. *hederacea* are included, and consequently the group has been designated as v. *hederacea.* Barton's original description has been extended to include all such plants, rather than only those

with the ivy leaf type of segment. The form *H. incrassata* f. *distorta* of Yamada has tentatively been assigned to this group. No authentic specimen was available for examination, but the figure (1941) shows the type of habit found among the members of v. *hederacea*.

Halimeda fragilis Taylor

Plate 3, Figure 2; Plate 5, Figure 10; Plate 6, Figure 1; Plate 7, Figure 1; Plate 8, Figure 1; Plate 9.

Halimeda fragilis Taylor, 1950, p. 88, Plate 48, Figure 2.

Plants compact, often cushion-like, to 8 cm tall including the rather small holdfast region, rhizoids not noticeably interlaced with sand particles; calcification heavy; color on drying white, cream or grayish-green, the surface dull; branches occurring in more than one plane with up to four arising from a single segment; basal segment generally inconspicuous, cylindrical to reniform; others brittle, frequently ribbed and sometimes keeled, occasionally cylindrical, these usually occurring as the basal segments of branches, sometimes subcuneate but more commonly subreniform to reniform, the lower margin truncate to auriculate, the upper margin entire to trilobed, to 9 mm long, 16 mm broad, and averaging 0.50–0.75 mm in thickness.

Cortex of three to four layers of utricles produced by successive dichotomies in the lateral branches of the medullary filaments; outermost utricles separating on decalcification, appearing rounded in surface view and at times thickened along the peripheral margin, 21–52 microns in surface diameter, (32–)43–81 microns long in section, borne two or four on each secondary utricle; secondary utricles usually not constricted at their origin; 15–46 microns broad.

Nodal medullary filaments remaining unfused, although adjacent filaments may adhere slightly; filament walls in this region usually rather extremely thickened and deeply pigmented.

Type specimen: Marshall Islands, Eniwetok Atoll, Taylor 46–394, 2 June, 1946 (MICH).

Ecological and geographical distribution: Collected from 2–57 meters depth in the North Pacific and the Indian Oceans.

Specimens examined: PACIFIC OCEAN. GILBERT ISLANDS, Onotoa, Moul 8246, 26 July, 1951 (WRT); Onotoa, Moul 8265, 26 July, 1951 (WRT); Onotoa, Moul 8409, 20 August, 1951 (WRT, as *H. orientalis*). MARSHALL ISLANDS, Bikini Atoll, Taylor 46–75, 26 March, 1946 (MICH); Bikini Atoll, Taylor 46–193B, 13 April, 1946 (MICH); Eniwetok Atoll, Taylor 46–394, 2 June, 1946 (MICH, *TYPE*).
INDIAN OCEAN. CARGADOS CARAJOS, Gardiner (BM, as *H. incrassata* f. *ovata*).

Macroscopically, *H. fragilis* is most frequently confused with *H. opuntia*, *H. gracilis*, and to a lesser extent with *H. bikinensis*. In all four species the cortex is formed essentially by dichotomies in the lateral medullary filament branches, and thus internally there are also similarities. Difficulties in macroscopic determination, however, can always be resolved by an examination of the nodal medullary filaments, these remaining separate in *H. fragilis*, but fusing in twos and threes in the other species. The disjunct peripheral utricles in *H. fragilis* are also distinctive. In *H. bikinensis* these separate only with pressure, whereas they generally remain attached in *H. opuntia* and *H. gracilis*.

From *H. micronesica,* a second species in which the nodal filaments remain separate, *H. fragilis* can be distinguished macroscopically by its heavier calcification and by its often complanate branching. Its segments are somewhat thicker, larger, more brittle, and commonly reniform in shape rather than discoid or trilobed. In addition, the lowermost segment is usually smaller than the others rather than being generally much larger and flabellate as is typical for *H. micronesica.*

Halimeda micronesica Yamada

Plate 3, Figure 1; Plate 5, Figures 13–14; Plate 6, Figure 2; Plate 9.

Halimeda micronesica Yamada, 1941, p. 121, Figure 15; Yamada, 1944a, p. 29, Plate 5; Taylor, 1950, p. 89, Plate 46, Figure 2; Plate 47.

Halimeda orientalis Gilbert, 1947, p. 126, Figure 1.

?*Halimeda incrassata* f. *pusilla* Barton 1901, p. 28, Plate 4, Figure 44.

Plants compact, spreading, to 10 cm tall excluding the rhizoidal region which is often small but sometimes long and fibrous, the rhizoids not noticeably interlaced with sand particles; calcification moderate; color on drying white or steel-gray, the surface usually dull; branching, except for the basal region, mainly trichotomous and complanate; basal segment larger than the others and more or less reniform, its outer margin frequently undulate, to 12 mm long, 18 mm broad, supporting numerous cylindrical to subcuneate segments; other segments occasionally slightly ribbed, sometimes cylindrical but more commonly subcuneate to discoidal, the upper margin entire to trilobed, to 7 mm long, 9 mm broad and averaging to 0.5 mm in thickness.

Cortex mainly of three or occasionally four layers of utricles produced by successive dichotomies in the lateral branches of the medullary filaments; outermost utricles usually separating on decalcification but in young segments often slightly attached, usually appearing rounded in surface view, 28–48(–55) microns in surface diameter, 40–82 (–94) microns long in section, borne two or four on each secondary utricle; secondary utricles generally not constricted at their origin, 15–45 microns broad.

Nodal medullary filaments remaining unfused, although sometimes adhering slightly with adjacent ones; filament walls in this region thickened, and usually somewhat pigmented.

Type locality: Ants Atoll, near Ponape Island in the East Caroline Islands.

Ecological and geographical distribution: Occurring below low-tide level in lagoons and deeper reef pools, with a single, rather delicate specimen dredged from 37 meters depth; known from the North and South Pacific and the Indian Oceans.

Specimens examined: PACIFIC OCEAN. MARSHALL ISLANDS, Bikini Atoll, Taylor 46–47, 18 March, 1946 (MICH); Bikini Atoll, Taylor 46–220, 18 April, 1946 (MICH); Bikini Atoll, Taylor 46–226, 16 April, 1946 (MICH); Rongelap Atoll, Taylor 46–457, 16 June, 1946 (MICH); Rongelap Atoll, Taylor 46–471, 21 June, 1946 (MICH, as *H. orientalis* forma). CAROLINE ISLANDS, Yamada, January, 1939 (WRT, *TYPE*). PHILIPPINES, Basilan Island, Ebalo, A-20, January, 1941 (MICH, *TYPE* of *H. orientalis*). SUMATRA, Kostermans 731a, October, 1938 (MICH, as *H. orientalis*). BINONGKO ISLAND, Siboga Expedition (NY, as *H. incrassata* f. *pusilla*). PENRHYN ISLAND, Crocker 40, 19 September, 1936 (UC 633985).

INDIAN OCEAN. SEYCHELLES ISLANDS, Gardiner (BM, as *H. incrassata* f. *ovata*).

This was the first species described in which the medullary filaments continued unfused throughout the node. Barton (1901) mentioned such a condition but felt that it occurred largely in stunted plants, assigning many such specimens to *H. incrassata* f. *ovata.*

In addition to having this type of nodal behavior, *H. micronesica* is characterized by peripheral utricles which usually separate readily, and by an extremely modified basal, rarely suprabasal, segment which may become very large in certain specimens but appears somewhat less distinctive in others. In well-developed plants a somewhat prostrate manner of growth is indicated by branches projecting in all lateral directions from this one segment. These branches occasionally terminate in rope-like extensions, to approximately 6 cm in length, which consist of intertwined rhizoidal filaments. The dichotomous organization of the cortex and the tendency of the peripheral utricles to remain slightly attached in apical segments has been discussed in the section on morphology and anatomy.

A comparison of *H. micronesica* with *H. orientalis* which also has separate nodal filaments, revealed no critical differences in histological characteristics, this latter species also possessing a flabellate basal segment although it frequently is not as well developed as in *H. micronesica.* The apparent differences, the bluish-gray color at the branch tips in *H. orientalis* as opposed to whitish in *H. micronesica,* and the thinner, predominantly discoidal segments in the upper two-thirds of the plant rather than trilobed ones, can partly be attributed to age differences, the specimens of *H. orientalis* available for study generally appearing rather immature. These differences would seem to fall within the normal range of variation of this species. Thus, since no significant differences could be found between the two species, *H. orientalis,* the more recently described, has been placed in synonymy under *H. micronesica.*

Halimeda incrassata (Ellis) Lamouroux

Plate 4, Figures 1–2; Plate 5, Figure 21; Plate 6, Figures 21–24; Plate 12.

Corallina incrassata Ellis, 1767, Plate 17, Figures 20–27; Ellis and Solander, 1786; p. 111, Plate 20, Figures D_{1-6}, d, d_{1-3}.

Corallina tridens Ellis and Solander, 1786, p. 109, Plate 20, Figure a.

Halimedea incrassata Lamouroux, 1812, p. 186; *Halimeda incrassata* Lamouroux, 1816, p. 307; Barton, 1901, p. 25, Plate 4, Figures 39, 41–51.

Halimeda incrassata f. *gracilis* Børgesen, 1911, p. 141, Figure 8; Børgesen, 1913, p. 111, Figure 89.

Halimeda incrassata f. *lamourouxii* J. Agardh, 1887, p. 86; Barton, 1901, p. 27, Plate 4, Figure 41.

Halimeda incrassata f. *ovata* J. Agardh, 1887, p. 86; Barton, 1901, p. 27, Plate 4, Figures 42, 47.

Halimeda incrassata f. *rotunda* Barton, 1901, p. 28, Plate 4, Figure 45.

?*Halimeda incrassata* f. *tridentata* Duchassaing *ex* J. Agardh, 1887, p. 86.

Halimeda incrassata f. *tripartita* Barton, 1901, p. 27, Plate 4, Figure 43.

Halimedea tridens Lamouroux, 1812, p. 186; *Halimeda tridens* Lamaroux, 1816, p. 308; Collins, 1909–18, p. 398; Taylor, 1928, p. 84, Plate 10, Figure 14; Taylor, 1950, p. 92.

?*Halimeda brevicaulis* Kützing, 1858, p. 11, Plate 25, Figure 2.

Plants occasionally lax in habit, but more commonly erect and compact, to 24 cm

tall excluding the holdfast region, which may extend to 9 cm in length; calcification rather heavy at the base, becoming moderate to light in the middle and upper portions; color on drying copper to greenish-white or cream, the surface generally dull; branching mainly di- to tetrachotomous, the lower part of the plant often remaining simple for some distance, or branching immediately above the first to second basal segments, the resultant segments at times becoming consolidated laterally into a rather massive fan-shaped structure; the basal first to second segments cylindrical to subcuneate, others plane, ribbed or keeled, shape variable, from cylindrical to reniform, the outer margin entire, undulating or deeply lobed, to 10 mm long, 14 mm broad, and averaging 0.75–1.00 mm in thickness.

Cortex of three to five layers of utricles; the outermost utricles generally remaining attached after decalcification for an average distance of 12 microns, their lateral and peripheral walls occasionally thickened, (34–)45–85(–105) microns in surface diameter, (40–) 50–95(–125) microns long in section, two or four supported on each secondary utricle; secondary utricles often globose or subglobose, 23–70(–95) microns broad, 30–90(–118) microns long; innermost utricles (32–)46–100(–150) microns broad.

Nodal medullary filaments uniting as a single group for a distance of approximately 25–80 microns, the adjacent filaments communicating by pores or tubular processes; walls in this region thickened and often deeply pigmented.

Type specimen: Collected by Ellis in Jamaica; according to Barton (1901) this specimen has been lost.

Ecological and geographical distribution: Common in shallow water but also extending to at least 30 meters depth; frequently collected among sea grasses on sand flats; pantropical.

Representative specimens examined: ATLANTIC OCEAN. CURACAO ISLAND, Taylor 39–568, 23 April, 1939 (MICH). PANAMA, Caledonia Harbor, Taylor 39–169a, 3 April, 1939 (MICH). BRITISH HONDURAS, Schipp A 119a, 9 May, 1933 (MICH, all as *H. tridens*). MARTINIQUE, Hamel and Hamel-Joukov 57, March, 1930 (BM, MICH). GUADALOUPE, Feldmann 3651, 7 April, 1936 (MICH, fertile). VIRGIN ISLANDS, Børgesen, 1905–06 (NY, as *H. incrassata* f. *gracilis*). PUERTO RICO, Howe, 4424, 22 March, 1906 (NY, fertile); Howe 7300, 1 July, 1915 (NY, fertile, both as *H. tridens*). HAITI, Bartlett 17853, 1 May, 1941 (MICH, as *H. tridens*). SOUTH CAICOS ISLANDS, Howe 5605, 18 December, 1907 (NY). JAMAICA, Howe 4903, 8 January, 1907 (NY, both as *H. tridens*). CUBA, Dawson 7593, 10 May, 1949 (MICH, as *H. tridens*). BAHAMAS, Howe 5130, 28 November, 1907 (NY, fertile); Howe 5531, 12 December, 1907 (NY, fertile, both as *H. tridens*). FLORIDA, Taylor 897, 21 June, 1925 (NY, fertile, as *H. tridens*). BERMUDA, Bernatowicz 49–1950, 5 June, 1949 (MICH, as *H. tridens*).

NORTH PACIFIC OCEAN. GILBERT ISLANDS, Onotoa, Moul and Cloud 8468, 25 August, 1951 (WRT, as *H. tridens*). MARSHALL ISLANDS, Bikini Atoll, Taylor 46–189B, 13 April, 1946 (MICH, as *H. tridens* f. *tripartita*). RYUKYU ISLANDS, Anon., *ex* herb. Okamura (UC 418091). PHILIPPINES, Sulu Archipelago, Bartlett 16033, 15 September, 1935 (MICH, as *H. tridens*). JAVA, Kostermans 616, 16 October, 1938 (MICH, as *H. tridens*).

SOUTH PACIFIC OCEAN. MARQUESAS ISLANDS, Crossland 6749, 21 January, 1925 (UC 667658, as *H. tridens* v. *ovata*). SOCIETY ISLANDS, Setchell and Parks

5256, 11 July, 1922 (UC 262718, as *H. simulans*). COOK ISLANDS, Parks, 1929 (UC 634174, as *H. tridens*). TONGA ISLANDS, Setchell and Parks, 17154, 9 August, 1926 (UC 667613, as *H. tridens*). SAMOA, Setchell 1129, 15 June, 1920 (UC 233551, as *H. tridens*). SOLOMON ISLANDS, Crocker 0654B, 8 June, 1933 (UC 513212, as *H. tridens* v. *ovata*). NEW GUINEA, Heydreich 44 (NY, as *H. tridens*).

INDIAN OCEAN. SEYCHELLES ISLANDS, Praslin Reef, Gardiner (BM). AFRICA, Zanzibar, Anon., *ex* herb. Pike (NY, as *H. opuntia*).

The earlier synonymy has been listed by Barton (1901).

The extreme variability of the segments of this species led to its consideration as two distinct entities by the early workers who relied almost entirely on macroscopic criteria. Consequently, specimens with predominantly subcuneate or discoidal segments were referred to as *H. incrassata,* those with many tridentate ones as *H. tridens.* Harvey, in 1858, suggested that these were possibly only varieties of the same species, but he and later workers continued to refer to them as distinct entities. Finally, in 1901, in the publications of two independent workers, Collins and Barton, the two species were united, Collins whose work appeared a month earlier choosing the epithet *tridens,* Barton the epithet *incrassata.* Subsequently both names have been employed in referring to this single species, North Americans choosing *tridens,* Europeans and Asiatics, *incrassata.* Howe (1907, footnote p. 501) based his choice of *tridens* on the nomenclatorial principle that when species published within the same work are united, the legitimate epithet is that chosen by the first worker which would be Collins. This favors *tridens* by a narrow margin. Børgesen (1911) less validly defended the use of *incrassata.* Both he and Howe considered Ellis and Solander (1786) to be the source of the original description and plates. Ellis, however, in 1767, in a published letter to Linnaeus, included excellent illustrations of the habit and certain microscopic details of a plant he referred to as *H. incrassata,* the drawings appearing very similar to those of the later work (1786). Although no formal description is provided in the 1767 publication, the figures with the analysis of parts and accompanying legend seem to fulfill the requirements for valid publication stated in the Paris Code (Lanjouw, 1956, Article 43). Consequently, the epithet *incrassata* has been given priority over *tridens.*

A total of eight forms have been designated for this species: f. *lamourouxii* J. Agardh (1887), f. *ovata* J. Agardh (1887), f. *tridentata* Duchassaing *ex* J. Agardh (1887), f. *pusilla* Barton (1901), f. *rotunda* Barton (1901), f. *tripartita* Barton (1901), f. *gracilis* Børgesen (1911), and f. *distorta* Yamada (1941). Of these f. *gracilis* represents rather lax plants in which the predominating segment type is that embodied in the original concept of *H. incrassata*; f. *tripartita* includes those specimens in which the common shape is an extreme modification of the *tridens* type, whereas f. *rotunda* consists of relatively small plants, often from moderate depths, with discoid to reniform segments. This latter form is at times confused with *H. simulans,* but can be distinguished from it by its greenish-white or brownish-white segments, those of *H. simulans* appearing yellowish-green, and by the larger average diameters of its peripheral utricles. Since these forms mainly represent external modifications unaccompanied by significant histological differences they have not been given separate taxonomic standing. A fourth form, f. *tridentata* has been tentatively placed in synonymy based on the information given by Barton concerning this taxon.

From the photographs in the New York Botanical Garden Herbarium of the type

specimens of f. *lamourouxii* and f. *ovata*, these plants being deposited in the Lund Herbarium in Sweden, it would seem that the first is probably a somewhat weather-beaten typical plant, and the second an immature Pacific specimen. These epithets often appear to be somewhat indiscriminately employed, the plant figured by Barton as f. *lamourouxii* (1901, Plate 4, Figure 41) appearing rather different from the above photograph although it too would seem to fall within the limits of the typical *H. incrassata*. The epithet *ovata* has by many workers been applied to the rather immature plants from the Pacific which have large well-developed basal segments surmounted by numerous small shrivelled ones, whereas Barton's concept of this taxon was very broad as evidenced from her description of the form (1901, p. 27), and from specimens in the British Museum annotated as such by her, but which are a number of other species including *H. fragilis* and *H. micronesica*, the two species with separate nodal filaments.

Among the remaining forms, the fragment of f. *pusilla* examined appeared very similar to *H. micronesica*. The source of this material was the Siboga Expedition; so it may represent a portion of the type specimen. It thus seems likely that this form is misplaced in the taxonomy of *H. incrassata*, as may also be the case for f. *distorta*. The habit shown in Yamada's illustration (1941) suggests *H. opuntia* v. *hederacea*.

The species *H. brevicaulis* has been placed tentatively in synonymy on the bases of the figure given by Kützing (1858) and of Howe's identification of a fragment of type material as probably representing a lax condition of *H. tridens* (Howe 1905b, Addendum, p. 586). The plant he examined was from the Sonder Herbarium which is deposited in the National Herbarium of Australia at Victoria. The type locality for this species is the Bahamas.

Certain modifications other than those of segment shape occur among specimens of *H. incrassata*. These include an increase in the number or height of the cortical layers, either or both conditions producing thicker segments as was discussed in the section on anatomy. The firmness of the connections between the nodal medullary filaments also varies, the constituent filaments at times communicating mainly by a restricted number of narrow tubular processes which may be relatively easily severed, rather than by numerous well-developed pores or broad tubes. In addition, the general appearance of the basal portion of the plant may differ. Many specimens from the Caribbean often appear distinctly caulescent, whereas in older plants from this region the lower branches or cauline units may consolidate laterally to form a fan-shaped structure. The stipe region in many Pacific specimens is generally restricted to one or two subcylindrical to subcuneate segments, the upper one supporting several branches.

Halimeda simulans Howe

Plate 3, Figure 4; Plate 5, Figure 27; Plate 6, Figure 15; Plate 11.

Halimeda simulans Howe, 1907, p. 503, Plate 29; Collins, 1909–18, p. 401; Taylor, 1928, p. 84, Plate 10, Figure 12; Plate 11, Figures 18–19.

Halimeda incrassata v. *simulans* Børgesen, 1911, p. 144, Figure 11; Børgesen, 1913, p. 114, Figure 92.

Plants compact, forming cushion-like clumps, to 12 cm tall excluding the holdfast region which may extend to 4 cm; calcification moderately heavy, decreasing towards the apex; color on drying cream to greenish, the surface dull to somewhat glossy; branching complanate, frequent, mainly di- to tetrachotomous; stalk region sometimes mod-

erately well-developed, resulting from the fusion of small adjacent segments, more commonly short and rather inconspicuous, of two to three cylindrical to subcuneate or at times reniform segments, the upper one supporting several subcuneate segments often in an imbricated fashion; other segments frequently ribbed, occasionally cylindrical but more commonly subcuneate to reniform, the outer margin entire, undulating or shallowly lobed, to 11 mm long, 15 mm broad, and averaging 0.75–1.00 mm in thickness.

Cortex of two to four layers of utricles with a fifth zone occasionally present; outermost utricles generally remaining attached after decalcification for an average distance of 7 microns, (26–)31–60 microns in surface diameter, 30–60(–90) microns long in section, two or four supported by each secondary utricle; secondary utricles 25–60(–78) microns broad, 28–70(–110) microns long; innermost utricles (34–)40–90 microns broad.

Nodal medullary filaments uniting as a single group for a distance of approximately 25–55 microns, the adjacent filaments communicating by pores; walls in this region thickened and pigmented.

Type specimen: Puerto Rico, Culebra Island, Howe 4332, 6 March, 1906 (NY).

Ecological and geographical distribution: Extending from near low-tide level to at least 30 meters depth; most commonly collected on sand or sand-covered rocks; known from the North and South Atlantic and Pacific Oceans.

Representative specimens examined: NORTH ATLANTIC OCEAN. PANAMA. Colon, Howe 6777, 6 January, 1910 (NY); Caledonia Harbor, Taylor 39–160, 3 April, 1939 (MICH). BRITISH HONDURAS, near Belize, Lundell 70, autumn, 1929 (NY). MARTINIQUE, Hamel 81, March, 1930 (NY). DOMINICA, Taylor 56–61, 28 March, 1956 (WRT). VIRGIN ISLANDS, Børgesen, 1905–06 (NY). PUERTO RICO, Howe 4332, 6 March, 1906 (NY, *TYPE*); Howe 7202, 27 June, 1915 (NY); Howe 7302, 1 July, 1915 (NY). SOUTH CAICOS ISLANDS. Howe 5543a, 15 December, 1907 (NY). JAMAICA. Howe 4845, 7 January, 1907 (NY); Howe 5885, 25 February, 1909 (NY). CUBA, Henderson and Bartsch, 8–9 June, 1914 (NY). BAHAMAS, Howe 3561, 30 January, 1905 (NY); Howe 5757, 24 December, 1907 (NY). FLORIDA, Dry Tortugas, Taylor 233, 10 July, 1924 (WRT, slightly fertile); Boot Key, Howe 6577, 9 April, 1909 (NY).

SOUTH ATLANTIC OCEAN. FERNANDO NORONHA ISLAND. Williams, 9 March, 1945 (UC 761005). BRAZIL. south of Recife, Williams, February, 1945 (DUKE).

PACIFIC OCEAN. SOCIETY ISLANDS. Setchell and Parks 5129, 5 June, 1922 (NY, UC 261374); Setchell and Parks 5254, 11 July, 1922 (BM, NY, UC 262717). SOLOMON ISLANDS, Crocker 0677c, 21 June, 1933 (UC 513209). SANTA CRUZ ISLANDS, Crocker 0716, 10 July, 1933 (UC 513214). MARSHALL ISLANDS. Bikini Atoll, Taylor 46–118, 1 April, 1946 (MICH, as *H. tridens*).

This species, although closely related to *H. incrassata*, seems sufficiently distinct from it to merit specific rank. The substipitate or occasionally stipitate habit, with the basal segments of the lowermost branches commonly imbricated, is fairly distinctive of *H. simulans*, this being particularly different from the habit of mature Atlantic specimens of *H. incrassata*. Other distinguishing characteristics are the predominating greenish-cream, reniform or slightly trilobed segments and the smaller diameters of the peripheral utricles, these averaging 45 microns as compared to 73 microns in *H. incrassata*. In the latter species these utricles adhere more firmly, whereas in *H. simulans* the corners often appear slightly rounded in surface view, the utricles nevertheless usually remaining at-

tached. The pores between adjacent nodal medullary filaments in *H. simulans* may at times be relatively small and consequently not particularly conspicuous in longitudinal sections. Their presence in such cases is more easily demonstrated by transverse sections through the node.

The reniform segments of this species sometimes lead to confusion with *H. tuna* from which it is entirely distinct microscopically. Characteristics of habit, segment color, the tendency for segments to be lobed in *H. simulans* rather than entire as in *H. tuna*, and the occurrence of a usually more extensively developed holdfast, will usually suffice to distinguish these two species macroscopically.

Halimeda favulosa Howe

Plate 4, Figure 5; Plate 5, Figure 24; Plate 6, Figure 20; Plate 8, Figures 2–4; Plate 12.

Halimeda favulosa Howe, 1905b, p. 563, Plate 23, Figure 2; Plate 24; Plate 26, Figures 1–6; Collins, 1909–18, p. 401.

Plants attenuate, suberect or somewhat flaccid, to 22 cm tall excluding the holdfast, which is moderately well-developed; calcification moderate; color on drying white, cream or greenish, the surface dull, rugose and appearing pitted; branching sparse, mainly ditrichotomous; basal segments commonly compressed-cylindrical to trapezoidal, often forming a short stipe and supporting several segments which remain separate or consolidate laterally, either entirely or in part, to form a fan-shaped unit; other segments friable, cylindrical to subcuneate, the upper margin two to five lobed, the resultant arms compressed or terete, to 9 mm long, 13 mm broad and averaging 1.0–1.5 mm in thickness.

Cortex of two to three layers of utricles; outermost utricles (110–)125–220(–260) microns in surface diameter, 170–280(–400) microns long in section, separating or remaining slightly attached after decalcification, appearing rounded in surface view, in section sometimes constricted basally forming a conspicuous bulb; one, two, or four supported by each secondary utricle; secondary utricles 100–150(–190) microns broad, 170–275(–424) microns long.

Nodal medullary filaments uniting as a single group for a distance of approximately 28–50 microns, the adjacent filaments communicating by pores; walls in this region thickened and pigmented.

Type specimen: Bahamas, Cave Cays, Exuma Chain, Howe 3981, 19 February, 1905 (NY).

Ecological and geographical distribution: From shallow water, appearing reclinate if exposed at low-tide; growing in sand, and often in close association with other members of the *H. incrassata* complex; of rather restricted distribution in the Caribbean.

Specimens examined: ATLANTIC OCEAN. BAHAMAS. Howe 3417b, 28 January, 1905 (NY); Howe 3421b, 28 January, 1905 (NY); Howe 3981, 19 February, 1905 (NY. *TYPE*); Howe 4186a, 26 February, 1905 (NY).

Since *H. favulosa* fairly closely resembles the relatively common *H. monile* and often grows in the same ecological association, it may easily be passed over as such in the field. This perhaps partly explains its extremely restricted recorded distribution.

In the laboratory this species can be distinguished macroscopically from *H. monile* and other members of the *H. incrassata* complex by the friable nature of its segments,

and by their pitted surface. The latter appearance results from the large diameters of the peripheral utricles, and their partial or complete separation by calcium carbonate partitions. Histologically, *H. favulosa* is characterized by a rather poorly developed inner cortex and by the large dimensions of the peripheral and secondary utricles. The differences between this taxon and *H. macrophysa* in which the segments also are friable and appear pitted, have been discussed in the taxonomic treatment of this second species.

In his 1905(b) paper, Howe figured and commented on the dense granular contents of some of the utricles and medullary filaments stating: "We have found no evidence that such parts become detached, but for some reason a reserve food supply seems to be concentrated in them." These regions in the plants he worked on may be fairly easily detected by dark green or black patches on the surface of some of the segments. Sections of such areas confirmed the conditions mentioned by Howe, often the entire medulla and cortex appearing golden or blackish because of the dense contents of their filaments. A closer examination of the surrounding segments revealed a few clusters of gametangia and sections from these segments showed the reserve material concentrated in the gametangia and their stalks, which now appeared golden or blackish, whereas the amounts of this food substance in the cortex and medulla were in general considerably smaller. In the cases observed, the gametophores seemed to originate mainly from the peripheral utricles. The arrangement of the gametangia on these stalks is discussed along with other details of their structure in the section on morphology and anatomy.

Halimeda monile (Ellis and Solander) Lamouroux

Plate 4, Figure 4; Plate 5, Figure 26; Plate 6, Figure 16; Plate 7, Figure 12; Plate 8, Figures 12–13; Plate 12.

Corallina monile Ellis and Solander, 1786, p. 110, Plate 20, Figure c.

Halimedea monile Lamouroux, 1812, p. 186; *Halimeda monile* Lamouroux, 1816, p. 306; Howe, 1907, p. 501; Collins, 1909–18, p. 399; Taylor, 1928, p. 82.

Halimeda incrassata v. *monilis* Harvey, 1858, p. 24; Børgesen, 1911, p. 138; Børgesen, 1913, p. 112.

Halimeda incrassata v. *monilis* f. *cylindrica* Børgesen, 1911, p. 143, Figure 10; Børgesen, 1913, p. 113, Figure 91.

Halimeda incrassata v. *monilis* f. *robusta* Børgesen, 1911, p. 143, Figure 9; Børgesen, 1913, p. 113, Figure 90.

Halimeda incrassata f. *monilis* Barton, 1901, p. 27, but not Plate 4, Figure 40.

Plants sometimes elongate and sparsely branched, but more commonly compact and robust, to 16 cm tall excluding the holdfast, which may extend to 4 cm in length; calcification moderate, becoming heavier towards the base; color on drying copper to greenish-cream or dark green, the surface somewhat glossy; branching mainly ditrichotomous; basal first to second segments forming a short stipe, generally cylindrical to subcylindrical but becoming almost semicircular in densely branched plants, these supporting two to several segments which may consolidate laterally into a modified fan-shaped structure; other segments plane or ribbed, generally trilobed with terete arms, or cylindrical, the former usually predominating in regions of branching, the latter in the upper part of the plant, cylindrical ones to 8 mm long, 3 mm broad and averaging 1.5 mm in diameter, others, excluding the modified basal ones, to 8 mm long and 8 mm broad.

Cortex of three to five layers of utricles; outermost utricles remaining attached after decalcification for an average distance of 6 microns, (23–)30–60(–74) microns in surface diameter, 48–95(–116) microns long in section, two or four supported by each secondary utricle; secondary utricles 23–70 microns broad, 23–100(–140) microns long; tertiary utricles 30–90 microns broad.

Nodal medullary filaments usually uniting in twos, threes or larger groups for a distance of approximately 49–80 microns, these units held together by short narrow tubular processes which are easily broken; filament walls thickened and pigmented.

Type specimen: Collected by Ellis in Jamaica; according to Barton (1901) this plant has been lost.

Ecological and geographical distribution: Mainly a shallow-water plant, extending from low-tide level where it at times is exposed, to at least 13 meters depth, with slender, sparsely branched plants usually from sheltered locations and deeper water, the rather robust specimens generally from more exposed situations; of fairly common occurrence in the North Atlantic.

Representative specimens examined: ATLANTIC OCEAN. TORTUGA ISLAND, Taylor 39–427, 13 April, 1939 (MICH). PANAMA, Caledonia Bay, Taylor 39–209, 3 April, 1939 (MICH). SAN ANDRES ISLAND, Proctor, 22–27 April, 1948 (MICH). BRITISH HONDURAS, Schipp A 118, 7 May, 1933 (MICH). VIRGIN ISLANDS, Børgesen, 1895–96 (NY, f. *cylindrica*); Børgesen, 1905–06 (NY, f. *robusta*). PUERTO RICO, Howe 7176, 27 June, 1915 (NY). HAITI, Bartlett 17854, 1 May, 1941 (MICH). SOUTH CAICOS ISLANDS, Howe 5541, 15 December, 1907 (NY, fertile). JAMAICA, Porten, 26 May, 1949 (MICH). BAHAMAS, Howe 5073, 23 November, 1907 (NY). FLORIDA, Taylor 1163, 7 June, 1926 (MICH). BERMUDA, Bernatowicz 49–2118, 23 August, 1949 (MICH); Bernotowicz 50–27, 7 November, 1950 (MICH).

As seen from the preceding list of synonymy this species has had a rather varied taxonomic history since it was first described by Ellis and Solander in 1786. The earlier synonymy is given by Barton who, in addition to considering *H. monile* as a form of *H. incrassata*, equated with it *H. cylindracea* Decaisne and *H. polydactylis* J. Agardh. Although cylindrical segments occur in species other than *H. monile*, the predominance of such in this species, together with the general form of the plants, usually enables this taxon, which seems specifically entirely distinct from *H. incrassata* and the other members of this complex, to be identified macroscopically. In doubtful cases, differences in nodal anatomy and in the diameters of the peripheral utricles, the latter averaging 46 microns in *H. monile* and 73 microns in *H. incrassata*, are diagnostic. The somewhat modified behavior of the nodal filaments in *H. monile* has been discussed in the section on morphology and anatomy.

Børgesen (1911) in delimiting two ecological modifications, f. *cylindrica* and f. *robusta* of v. *monilis*, mentioned the resemblance of his figure of f. *robusta* to the drawing by Ellis of *H. monile* (1786). This similarity, and the existence of many intermediates between f. *robusta* and f. *cylindrica*, which seem to be unaccompanied by significant histological differences, make the recognition of these as separate taxa seem unjustified.

The results of an extensive study of specimens labelled *H. monile*, indicated a separation into two groups on the bases of habit, histological characteristics, and geographical distribution, the latter being Indo-Pacific or Caribbean. The most striking difference was in nodal structure, the medullary filaments in Indo-Pacific plants uniting firmly

into a single unit or disk at the node, the adjacent filaments usually communicating by conspicuous pores, whereas in Caribbean plants the structure was that indicated above for *H. monile*. The peripheral utricles in specimens of Indo-Pacific distribution tended to separate on decalcification, were shorter, and generally had smaller surface diameters, these averaging 32 microns as against 46 microns for the Caribbean group. In habit, the Indo-Pacific plants were usually distinctly caulescent although a well-developed fan-shaped basal structure was often present in older plants, and the diameters of their segments decreased, often by more than half, from the base to the apex of the plant, producing an attenuate appearance. These differences seemed to justify the recognition of the Indo-Pacific group as a separate species, and the above characteristics were found to agree well with those of two putative species, *H. cylindracea* and *H. polydactylis*, both of which were included in the synonymy under v. *monilis* by Barton (1901). The Indo-Pacific plants have thus been described separately under *H. cylindracea*, the older of the two applicable epithets, the substantive *monile* being retained for the Caribbean plants.

Halimeda cylindracea Decaisne

Plate 4, Figure 3; Plate 5, Figures 22–23; Plate 6, Figure 19; Plate 7, Figure 13; Plate 12.

Halimeda cylindracea Decaisne, 1842, p. 103.
Halimeda polydactylis J. Agardh, 1887, p. 89.
Halimeda incrassata Harvey, 1860, p. 125 *p.p.* including Plate 125.
Halimeda incrassata f. *monilis* Barton, 1901, p. 27 *p.p.* including Plate 4, Figure 40.

Plants elongate, usually attenuated from base to apex, to 19 cm tall excluding the holdfast which may extend to 4 cm in length; calcification moderate to light becoming heavier towards the base; color on drying yellowish-white or white to pale green, the surface somewhat glossy; branching restricted, mainly ditrichotomous; basal segments cask-shaped, to 7 mm long, 12 mm broad and averaging 3–4 mm in thickness, forming a distinct terete or subterete stalk with the lower forkings often becoming consolidated laterally to form a fan-shaped structure in older plants; branch segments subcuneate with lobed upper margins, others generally plane and predominantly cylindrical, although at times becoming subspherical towards the plant apex, to 7 mm long, 4 mm broad and averaging 1.5 mm in thickness.

Cortex of three to five layers of utricles; outermost utricles tending to separate on decalcification, their lateral and peripheral walls sometimes thickened, 17–45(–55) microns in surface diameter, 24–62 microns long in section, two or four supported by each secondary utricle; secondary utricles 17–62 microns broad, 23–80(–100) microns long; tertiary utricles 30–90 microns broad.

Nodal medullary filaments uniting as a single group for a distance of approximately 34–72 microns, the adjacent filaments communicating by pores; walls in this region thickened and pigmented.

Type specimen: Madagascar, Nossi-Bé, Pervillé (PC).

Ecological and geographical distribution: Usually obtained from deep water, growing to at least 55 meters depth; known for the North and South Pacific, and the Indian Oceans.

Specimens examined: NORTH PACIFIC OCEAN. MARSHALL ISLANDS. Bikini

Atoll, Taylor 46–72, 28 March, 1946 (MICH); Bikini Atoll, Smith 47–43, July to August, 1947 (MICH, both as *H. monile*); Rongelap Atoll, Taylor 46–470, 16 June, 1946 (MICH); Rongelap Atoll, Taylor 46–507, 21 June, 1946 (MICH, both as *H. tridens* f. *tripartita*). RYUKYU ISLANDS, Higashi, 5 May, 1928 (WRT, as *H. tridens*). PHILIPPINES, Culion Island, Bartlett 15578, 27 July, 1935 (MICH, as *H. monile*; UC 766543, as *H. incrassata* v. *monilis* f. *cylindrica*).

SOUTH PACIFIC OCEAN. TONGA ISLANDS, Setchell and Parks 17023, June to August, 1926 (UC 667614); Setchell and Parks, 15 July, 1926 (UC 696309, as *H. moniliformis*); Harvey 93 (BM, as *H. incrassata* v. *monilis*). FIJI ISLANDS, Agassiz, 1898 (NY, as *H. polydactylis*). NEW HEBRIDES, Anon., *ex* herb Merrifield (BM, as *H. incrassata*). TORRES STRAITS, Moseley (BM, as *H. incrassata* v. *monilis*); Murray Islands, Clark, October (NY, UC 470334, as *H. incrassata*). AUSTRALIA, Banks and Solander, 1770 (BM); Cape York, Moseley (BM, both as *H. incrassata* v. *monilis*).

INDIAN OCEAN. MADAGASCAR, Nossi-Bé, Hildebrandt, September, 1879 (BM, as *H. incrassata* f. *monilis*; UC 434133, as *H. monile*).

This species was considered by Barton to be synonymous with *H. incrassata* f. *monilis*. The reasons for regarding it as a distinct entity have been discussed in the taxonomic treatment of *H. monile*.

Halimeda stuposa Taylor

Plate 3, Figure 5; Plate 5, Figure 25; Plate 6, Figure 18; Plate 7, Figure 11; Plate 11.

Halimeda stuposa Taylor, 1950, p. 90, Plate 43, Figure 1; Plate 49; Plate 50, Figure 2.

Plants rather small, thick-set, compact, to 10 cm tall excluding the holdfast which is often massive, this generally extending to 5 cm in length but on occasion to 13 cm; calcification moderate; color on drying golden or white to greenish-cream, the surface smooth; branching mainly ditrichotomous; basal segments subcuneate or compressed-cylindrical, often forming a stipe or else consolidating laterally with adjacent segments to form a short trunk-like structure; other segments plane or occasionally ribbed; subcylindrical or cylindrical, at times becoming subspherical towards the apex, the upper margins entire to slightly lobed, to 7 mm long, 11 mm broad and averaging 2 mm in thickness.

Cortex of three to five layers of utricles; outermost utricles separating slightly on decalcification or remaining attached for an average distance of 4 microns, their lateral and peripheral margins usually thickened, 21–48(–55) microns in surface diameter, 50–80(–100) microns long in section, two or more commonly four supported by each secondary utricle; secondary utricles (17–)25–50 microns broad, (23–)30–90(–125) microns long; tertiary utricles 38–65 microns broad.

Nodal medullary filaments uniting as a single group for a distance of approximately 30–50 microns, the adjacent filaments communicating by pores; walls in this region thickened and pigmented.

Type specimen: Marshall Islands, Rongelap Atoll, Naen Island, Taylor 46–591, 17 July, 1946 (MICH).

Ecological and geographical distribution: Mainly from shallow water but occasionally in deeper situations, usually growing in sand; known for the North Pacific and the Indian Oceans.

Specimens examined: PACIFIC OCEAN. MARSHALL ISLANDS, Bikini Atoll, Taylor 46–32A, 3 April, 1946 (MICH); Bikini Atoll, Taylor 46–134, 3 April, 1946 (MICH); Bikini Atoll, Taylor 46–148B, 3 April, 1946 (MICH); Bikini Atoll, Taylor 46–158B, 3 April, 1946 (MICH); Bikini Atoll, Taylor 46–221, 18 April, 1946 (MICH); Bikini Atoll, Taylor 46–252, 22 April, 1946 (MICH); Eniwetok Atoll, Taylor 46–362, 31 May, 1946 (MICH); Rongelap Atoll, Taylor 46–591, 17 July, 1946 (MICH, *TYPE*); Rogers and Cowan 1775, 29 August, 1946 (NY).

INDIAN OCEAN. SEYCHELLES ISLANDS, Coelivy Island, Gardiner (BM). CARGADOS CARAJOS SHOALS, Gardiner (BM, both as *H. monile*).

This member of the *H. incrassata* complex at times may seem to resemble *H. monile* and certain forms of *H. incrassata*, but can usually be identified macroscopically by its short, rather thick-set appearance, the thickness of the segments averaging two mm. Also characteristic are the infrequent occurrence of deeply trilobed segments, and the presence of relatively short cylindrical ones, their length rarely exceeding twice the diameter, unlike similar segments in *H. monile* and *H. cylindracea* which are in general at least four times as long as thick.

Histologically, the thickened walls of the peripheral utricles of *H. stuposa*, these tending to separate with pressure, are generally fairly conspicuous in mature segments, particularly as viewed from the surface. This thickening is extremely well-developed in basal segments where the utricles usually separate on decalcification. Towards the plant apex, the induration is less pronounced and the utricles remain more firmly attached after decalcification. Although such thickening may occur in other species, particularly in basal segments, it is generally not as constant a feature as in *H. stuposa*.

Halimeda macroloba Decaisne

Plate 3, Figure 3; Plate 5, Figures 19–20; Plate 6, Figure 17; Plate 12.

Halimeda macroloba Decaisne, 1841, p. 118; Decaisne, 1842, p. 91; Barton, 1901, p. 24, Plate 3, Figures 33–38.

Halimeda macroloba v. ecalcarea Weber-van Bosse, 1926, p. 88.

Plants erect, flat or somewhat bushy, to 23 cm tall excluding the holdfast which is usually well-developed and may extend to 5 cm in length; calcification moderate to rather light; color on drying copper or white, to greenish, the surface somewhat dull; branching relatively sparse, mainly ditrichotomous but often becoming polychotomous in the basal region; basal segments commonly compressed-cylindrical to trapezoidal, of a somewhat stipitate nature and supporting several segments which may remain separate or consolidate laterally, either entirely or in part, to form a fan-shaped unit which may lie flat or become somewhat undulated or folded; other segments plane or slightly ribbed, at times compressed-cylindrical but more commonly subcuneate, discoidal or subreniform, the upper margin entire, undulating or occasionally somewhat lobed, to 29 mm long, 40 mm broad and averaging 1 mm in thickness.

Cortex occasionally of two, but more commonly of three to four layers of utricles; outermost utricles separating on decalcification or remaining slightly attached, their lateral and peripheral margins occasionally thickened, 23–49 microns in surface diameter, (46–)62–110(–144) microns long in section, usually four or occasionally two supported by each secondary utricle; secondary utricles 20–58(–68) microns broad, (30–)40–80(–140) microns long; tertiary utricles 36–90(–110) microns broad.

Nodal medullary filaments uniting as a single group for a distance of approximately 44–80(–115) microns, the adjacent filaments communicating by pores; walls in this region thickened and pigmented.

Type specimen: Red Sea, Schimper 871, 1837; isotype material in several herbaria including the British Museum and the New York Botanical Garden.

Ecological and geographical distribution: From shallow water, growing in mud and sand; known for the North and South Pacific, and Indian Oceans.

Representative specimens examined: NORTH PACIFIC OCEAN. MARIANA ISLANDS, Thompson 1, 1912 (NY). RYUKYU ISLANDS, Yamada, 15 April, 1935 (NY). PHILIPPINES, Mindoro, Bartlett 13964, 12–17 May, 1935 (MICH, fertile); Merrill 9151, October, 1913 (NY). HAINAN ISLAND, Tseng 91, June, 1934 (UC 563852). MALAY PENINSULA, Burchill, 14 January, 1922 (UC 341527). MALAYA, Singapore, Anon. 323, 1899 (BM). JAVA, Palmer and Bryant 1312, 27 November, 1909 (NY). HOORN ISLAND, Kostermans 48, 27 September, 1938 (MICH, fertile). LESSER SUNDA ISLANDS, Bali, Setchell and Setchell BS 146, 7 June, 1929 (UC 624489). BORNEO, Wittrock and Nordstedt 339 (BM, NY). CELEBES, Setchell and Setchell M 485, 22 June, 1929 (UC 624486). MOLUCCAS ISLANDS, Martius (NY, as *H. discoidea*).

SOUTH PACIFIC OCEAN. SOCIETY ISLANDS, Crossland 7078, 23 October, 1928 (UC 341157). TONGA ISLANDS, Harvey 21 in part (BM). SAMOA ISLANDS, Setchell 1128, 15 June, 1920 (BM, NY). FIJI ISLANDS, Greenwood 2001, July, 1943 (UC 775463). ARU ISLAND, Moseley (BM).

INDIAN OCEAN. SEYCHELLES ISLANDS, Praslin Reef, Gardiner (BM). AFRICA, Dar es Salaam, Holst 1264, December, 1892 (BM); Zanzibar, Hildebrandt 1917, December, 1875 (BM, UC 434118). RED SEA, Dscheddam, Schimper 871 (BM, NY, *ISOTYPE*). ADEN, Ferguson 444 (BM). ANDAMAN ISLANDS, Anon., *ex* herb. Dickie (BM). CEYLON, Koenig (BM). MADAGASCAR, Nossi-Bé, Hildebrandt 34, June, 1879 (UC 434117).

This species can usually be distinguished macroscopically from other members of the *H. incrassata* complex by its broad, flat segments. These are relatively large, to 29 mm long and 40 mm broad, although in certain plants they do not exceed 11 mm in length and 20 mm in breadth. Histologically, the diameters of the utricles decrease towards the outer surface, those of the peripheral utricles being relatively small. In *H. macroloba,* but not in most other species of this complex, these outer utricles generally separate readily on decalcification, but in apical segments may remain somewhat attached, in such cases appearing hexagonal in surface view.

The degree of calcification in *H. macroloba* as in other Halimedae often varies with age, decreasing from base to apex, and seeming less in young plants. Consequently, the *v. ecalcarea* described by Weber-van Bosse (1926) for two uncalcified plants with undulating or folded segment margins seems untenable as a separate taxon.

This species is at times confused with *H. discoidea* and *H. taenicola,* two members of the *H. tuna* complex. Although doubtful specimens can readily be identified on histological grounds, macroscopic criteria are usually adequate. These include the extent of development of the holdfast region, the general appearance of the basal part of the plant, and the size, appearance and color of the segments. In *H. discoidea* and *H. taenicola,* large segments, although often present, are usually of restricted occurrence. They are, however, generally very common in *H. macroloba.* The concave segment surface is often

a rather conspicuous feature in *H. taenicola*, such being less common in *H. discoidea*, whereas in *H. macroloba* the surface is generally plane.

Species of Uncertain Systematic Position

Halimeda irregularis Lamouroux

Halimeda irregularis Lamouroux, 1816, p. 307, Figure 7.
Type locality: Antilles, West Indies.

The appearance of the fragment figured suggests *H. incrassata*.

Halimeda lessonii Bory *ex* Chauvin

Halimeda lessonii Bory *ex* Chauvin, 1842, p. 125.

A description appears to be lacking for this species which is listed by Chauvin as belonging to the genus *Halimeda*. Hence it is to be regarded as a *nomen nudum*. No locality is given in the reference cited above. A fragment from a plant in Thuret's Herbarium, referred to as the type, and collected in the Society Islands by Lesson, 1825, was sent to Howe in 1908 by Bornet, owner of the above-named herbarium. This fragment was identified as *H. discoidea*.

Halimeda nervata Zanardini

Halimeda nervata Zanardini, 1858, p. 289, Plate 12, Figure 2.
Type specimen: Collected by Portier in the Red Sea.

The figure suggests *H. opuntia*.

Halimeda papyracea Zanardini

Halimeda papyracea Zanardini, 1851, p. 37; Zanardini 1858, p. 288, Plate 13, Figure 2.
Type specimen: Collected by Portier in the Red Sea.

The type specimen alluded to by Barton, and which is apparently *H. tuna s.s.*, was collected by Beccari in Singapore and, thus, is not the plant upon which Zanardini based his description. Howe (1907) was unable to locate Portier's specimen but tentatively placed this species in synonymy under *H. discoidea*. Although the figure given by Zanardini (1858) is suggestive of this species, *H. papyracea* cannot be identified with certainty without an examination of Portier's plant.

Halimeda rectangularis J. Agardh

Halimeda rectangularis J. Agardh, 1894, p. 100.
Type locality: Australia.

No illustration of this plant could be found in the literature. This species probably belongs to the *H. incrassata* complex, its affinities seeming to be with *H. cylindracea*.

Summary

From a detailed study of the morphology and anatomy of this genus of green algae it is seen that macroscopic characteristics can be used extensively to delimit the species.

These characteristics include the general appearance of the specimen, the extent of development of the holdfast region, the shape of the lowermost one to six segments or internodes, and the predominating shapes and sizes of the other segments. Qualities of texture, color, and degree of calcification of the segments although useful for some species, are generally less satisfactory. All these external characteristics are influenced by the environment.

Histological features of taxonomic importance include the average diameter of peripheral utricles, the degree of their lateral attachment, and the number supported by each secondary utricle. The second of these in particular, varies with the age of the segment. Thus, the peripheral utricles generally adhere more firmly in very young segments, whereas in the basal two to three segments, they may separate more readily than in the well-developed segments of the frond. The appearance and diameters of the inner cortical utricles, and the number of layers of utricles in the cortex are also definitive, both characteristics varying somewhat with the age of the segment. An additional histological feature, nodal anatomy, is of greater value in delimiting groups of species than individual species. It may be of three main types: (1) medullary filaments continuing unchanged throughout the node, (2) filaments fusing in small groups, most commonly in twos and threes for a distance of approximately 1.5 or several times the filament diameter, and (3) all or most of the filaments uniting into a single group for a short distance, the adjacent filaments communicating by thick-walled pores.

An analysis of the distribution maps for the 21 species shows the genus to be mainly tropical, the boundaries of this and the subtropical zone being delimited by the 25°C and 20°C isotheres, respectively. The exceptions are *H. tuna* which to a limited extent occurs also in the subtropics, and *H. cuneata* which is mainly restricted to the southern subtropics. The reported range of the latter species seems more extensive, however, because of specimens of *H. discoidea* frequently being misidentified for it. Four major categories of species distribution occur: (1) pantropical, with five species, (2) Indo-Pacific, seven species, (3) Pacific, four species, and (4) western Atlantic, four species. The five pantropical species, *H. discoidea, H. gracilis, H. opuntia, H. tuna,* and *H. incrassata,* represent two of the three main types of medullary filament behavior at the node, and give some insight into the phylogeny of the genus.

In the taxonomic revision of the genus 21 species, one variety, and one form are recognized, with *H. orientalis* being placed in synonymy under *H. micronesica,* and *H. cylindracea* being established as a species distinct from *H. monile.* Forma *hederacea* of *H. opuntia* is elevated to variety, f. *lata* transferred from *H. gracilis* to *H. lacunalis,* and the other varieties and forms placed in synonymy under the appropriate species. The priority of the species epithet *incrassata* over that of *tridens* is established. In arranging the species for discussion, attention is given where possible to interspecific relationships. The resulting clusters of possibly closely related species themselves fall mainly into two categories referred to as the *H. tuna* and *H. incrassata* complexes. These correspond to two of the main types of nodal behavior.

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PLATE 1

Habit Drawings

FIG. 1. *Halimeda lacunalis*, a specimen from the Marshall Islands.

FIG. 2. *Halimeda scabra*, a specimen from Florida.

FIG. 3. *Halimeda gigas*, habit of the type specimen, *Taylor* 46–419, from the Marshall Islands.

FIGS. 4–5. *Halimeda tuna*. Figure 4, a specimen from the Mediterranean. Figure 5, a specimen from the Pacific showing the large segments with undulate outer margins.

FIG. 6. *Halimeda cuneata*, a specimen from South Africa.

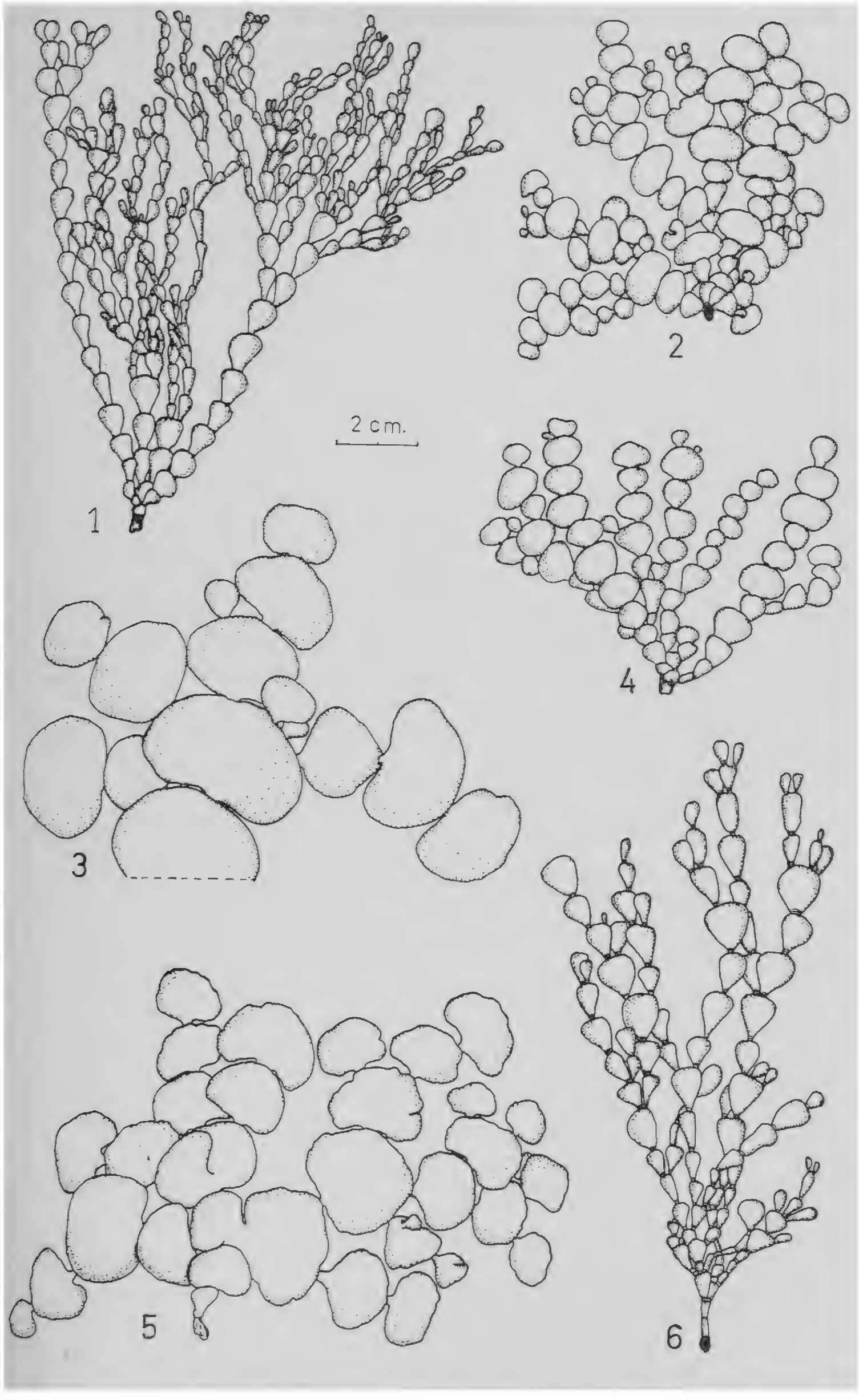
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PLATE 2

Habit Drawings

FIG. 1. *Halimeda bikinensis*, a specimen from the Marshall Islands.

FIG. 2. *Halimeda lacrimosa*, habit of the type specimen, *Howe 5524*, from the Bahamas.

FIG. 3. *Halimeda macrophysa*, a specimen from the Murray Islands, Torres Strait.

FIG. 4. *Halimeda gracilis*, a specimen from Saya de Malha, Indian Ocean.

FIG. 5. *Halimeda discoidea*, a specimen from the Philippines.

FIG. 6. *Halimeda taenicola*, a specimen from the Marshall Islands.

FIGS. 7–8. *Halimeda opuntia*. Figure 7. *Halimeda opuntia* v. *opuntia*, showing both the axial and lateral branch systems. Figure 8, *Halimeda opuntia* v. *opuntia*. Both specimens are from the Gilbert Islands.

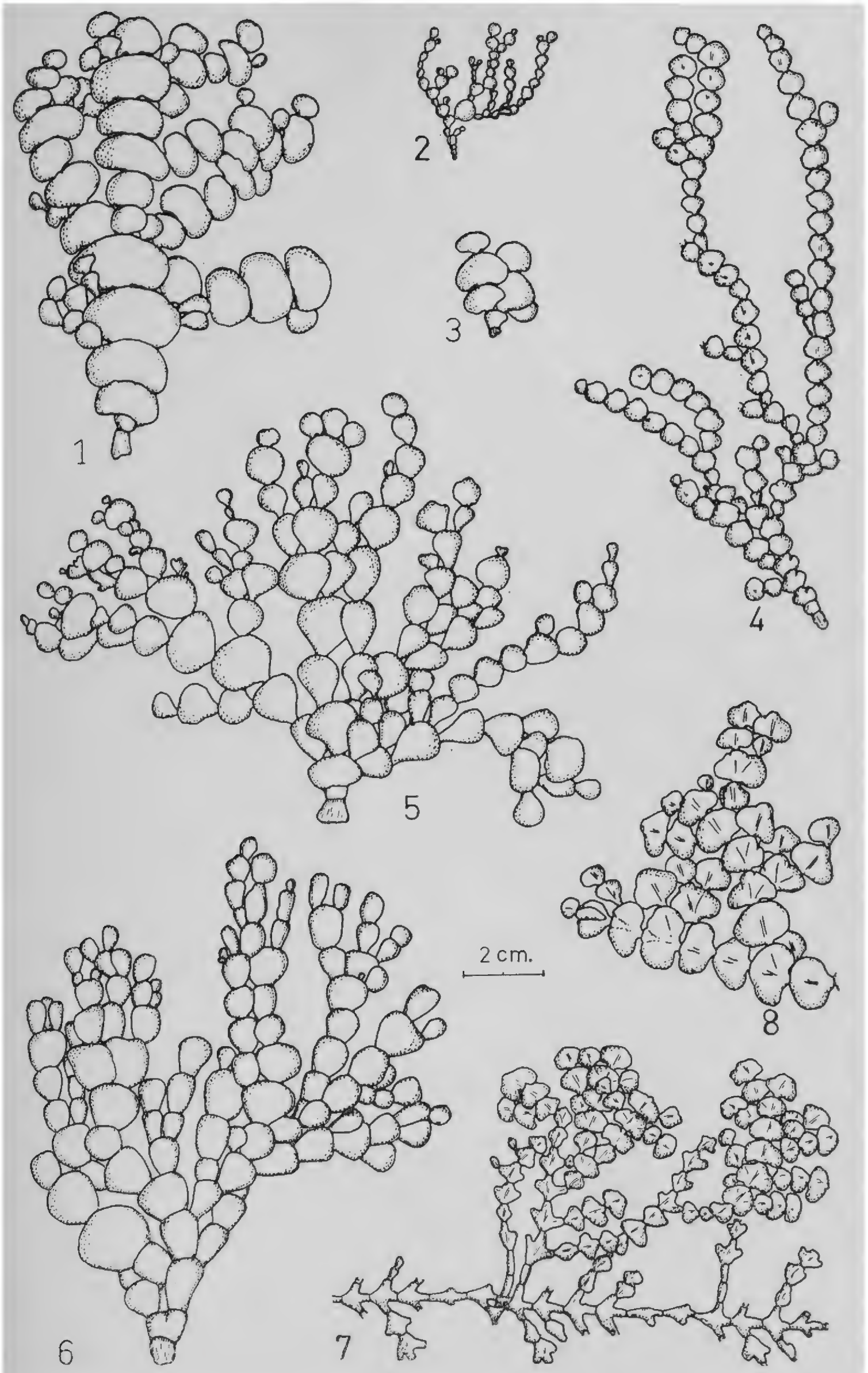
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PLATE 3

Habit Drawings

FIG. 1. *Halimeda micronesica*, a specimen from the Marshall Islands.

FIG. 2. *Halimeda fragilis*, a specimen from the Gilbert Islands.

FIG. 3. *Halimeda macroloba*, a specimen from Indonesia.

FIG. 4. *Halimeda simulans*, habit of the type specimen, *Howe 4332*, from Puerto Rico.

FIG. 5. *Halimeda stuposa*, a specimen from the Marshall Islands.

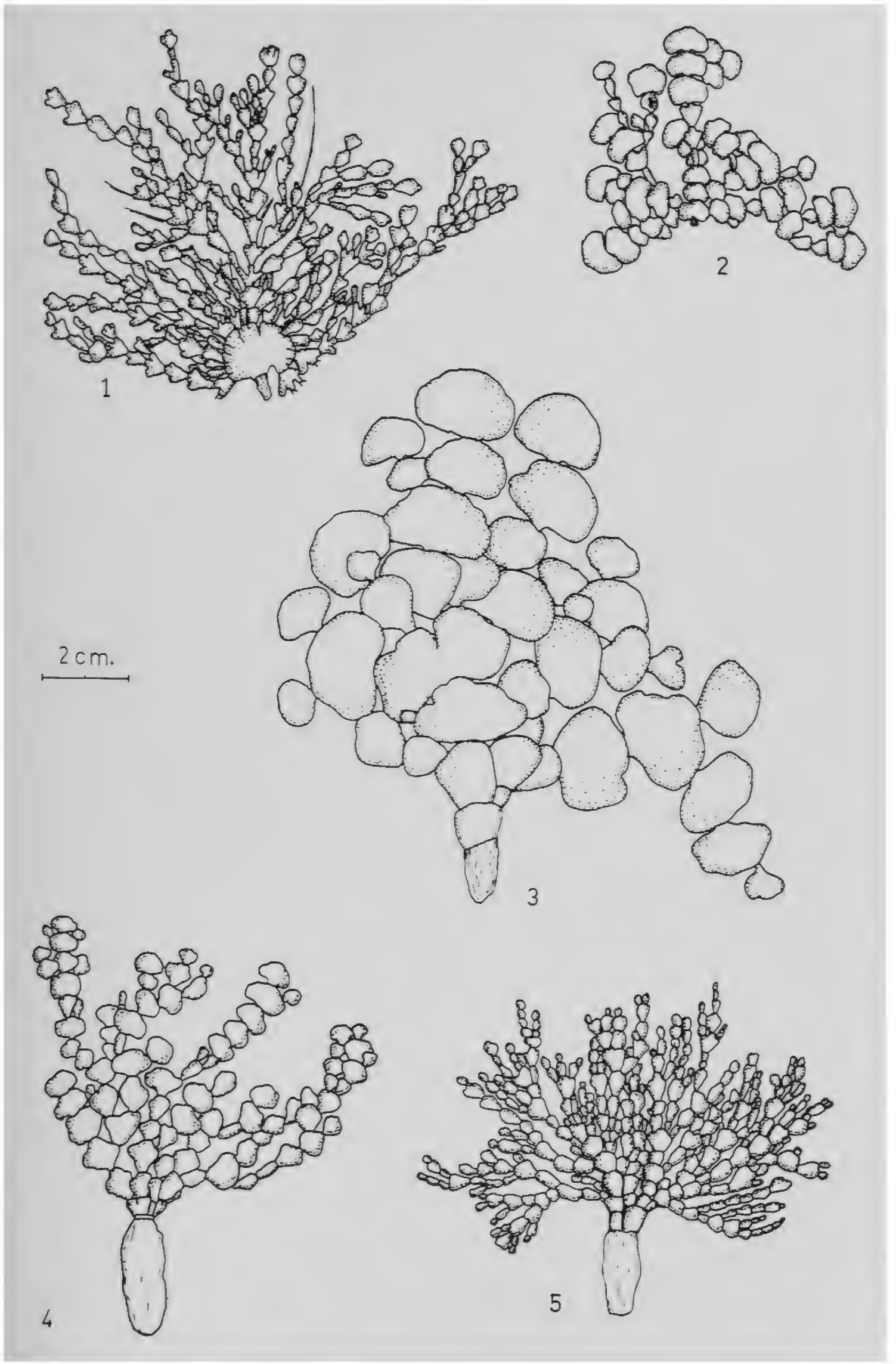
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PLATE 4

Habit Drawings

FIGS. 1–2. *Halimeda incrassata.* Figure 1, habit of a mature plant, showing the basal segments consolidated laterally into a fan-shaped structure. Figure 2, showing regeneration of branches from the basal fan-shaped structure.

FIG. 3. *Halimeda cylindracea,* a specimen from Madagascar.

FIG. 4. *Halimeda monile,* a specimen from Bermuda.

FIG. 5. *Halimeda favulosa,* habit of type specimen, *Howe 3981,* from the Bahamas.

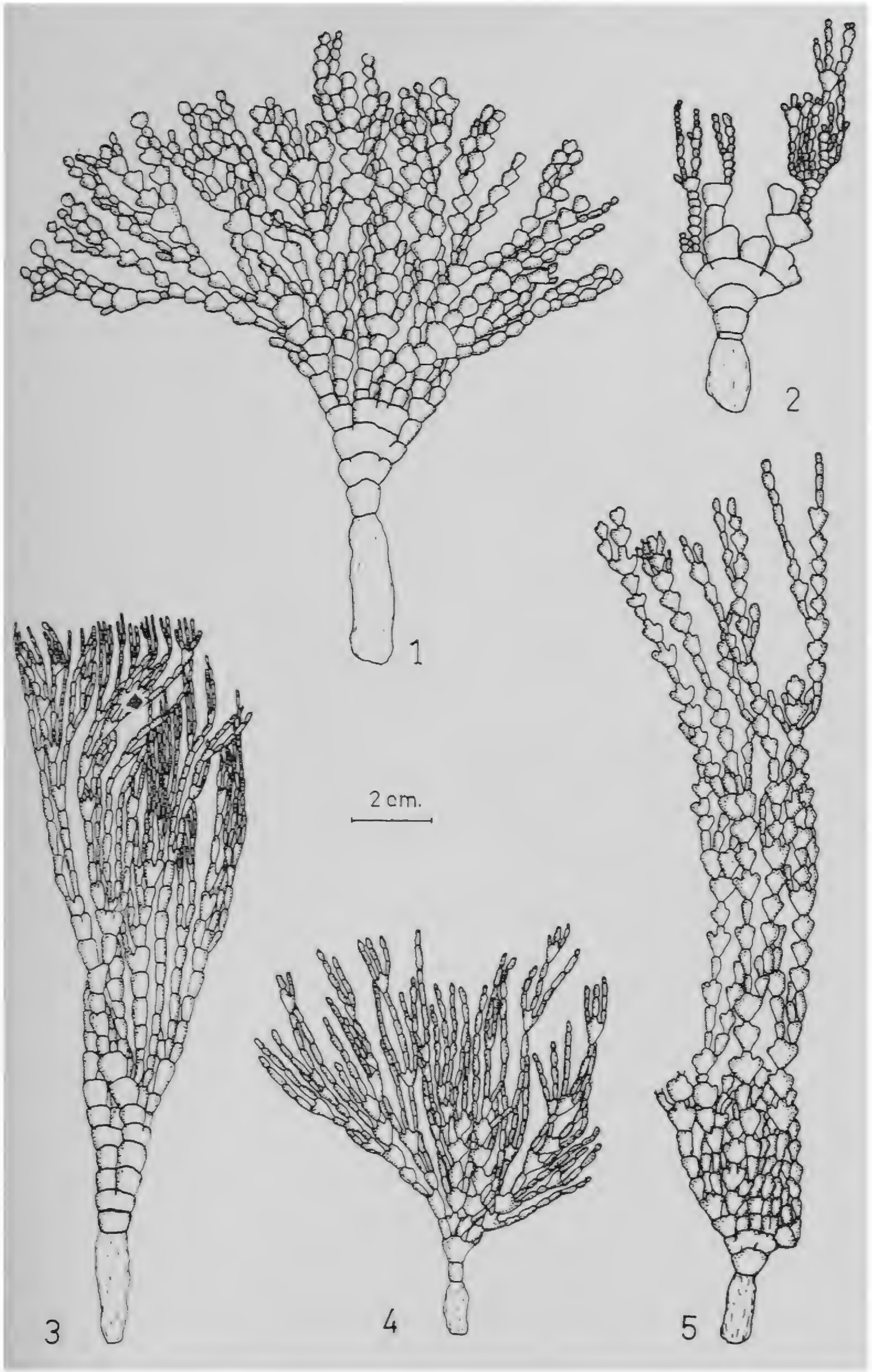
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PLATE 5

Surface View of the Peripheral Utricles

FIGS. 1–2. *Halimeda cuneata.* Figure 1, from a regular segment. Figure 2, from a cushion segment, showing the thickened walls which are fairly common in these small segments.

FIGS. 3–4. *Halimeda opuntia.* Figure 3, *Halimeda opuntia* v. *opuntia.* Figure 4. *Halimeda opuntia* v. *hederacea.*

FIG. 5. *Halimeda scabra.* The indurated spines are evident in surface view.

FIG. 6. *Halimeda lacunalis*

FIG. 7. *Halimeda gracilis*

FIG. 8. *Halimeda lacrimosa*

FIG. 9. *Halimeda tuna*

FIG. 10. *Halimeda fragilis*

FIG. 11. *Halimeda discoidea*

FIG. 12. *Halimeda taenicola*

FIGS. 13–14. *Halimeda micronesica.* Figure 13, from a mature segment. Figure 14, from a very young segment. The peripheral utricles adhere slightly.

FIG. 15. *Halimeda gigas*

FIG. 16. *Halimeda macrophysa*

FIGS. 17–18. *Halimeda bikinensis.* Figure 17, from a mature segment. Figure 18, from a very young segment. The peripheral utricles adhere slightly.

FIGS. 19–20. *Halimeda macroloba.* Figure 19, from a mature segment. Figure 20, from a young segment. Adjacent utricles adhere slightly.

FIG. 21. *Halimeda incrassata*

FIGS. 22–23. *Halimeda cylindracea.* Figure 22, from a mature segment. Figure 23, from a basal segments. The utricle walls are somewhat thickened.

FIG. 24. *Halimeda favulosa*

FIG. 25. *Halimeda stuposa*

FIG. 26. *Halimeda monile*

FIG. 27. *Halimeda simulans*

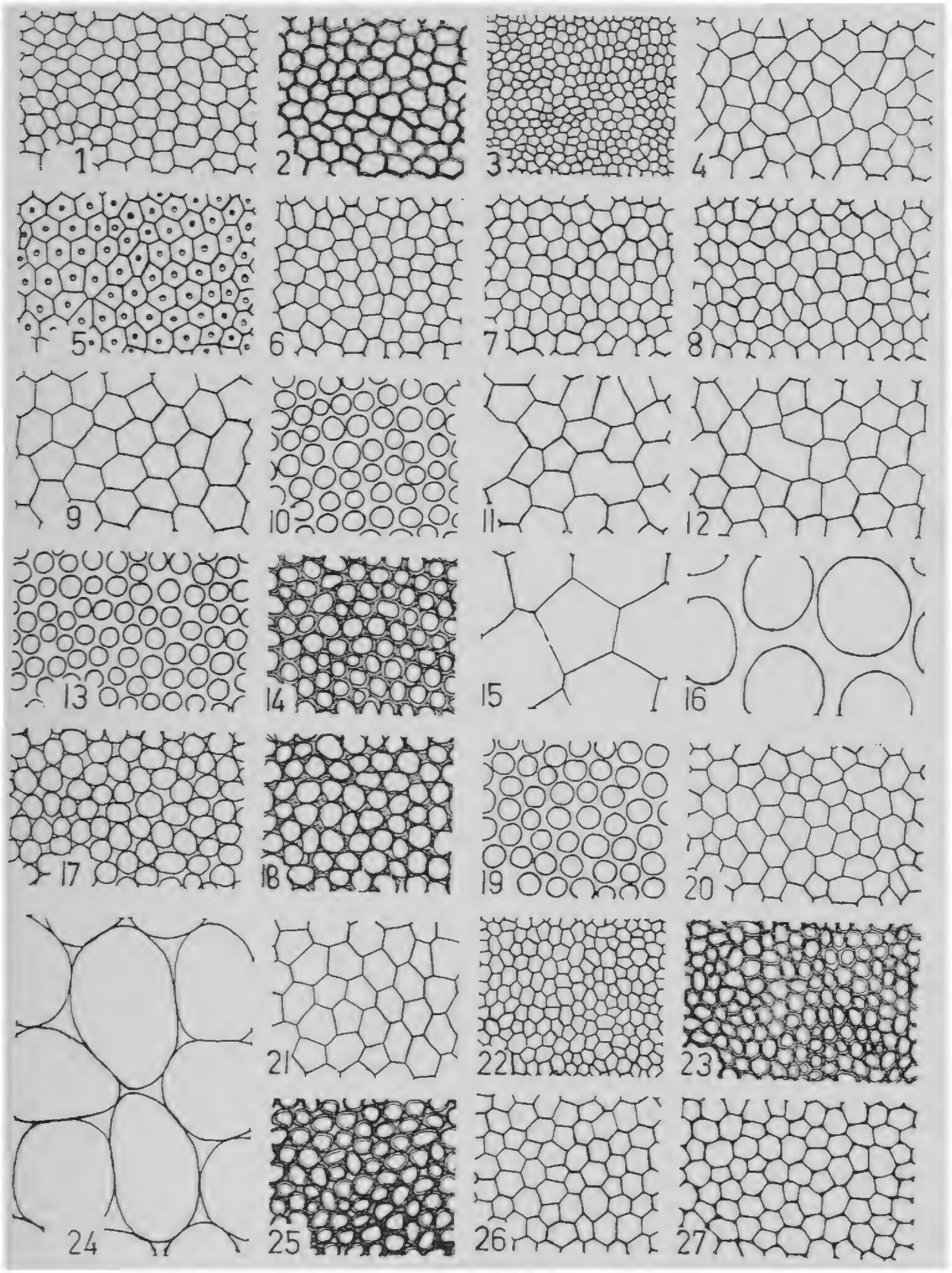
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PLATE 6

Sagittal Sections Showing the Structure of the Cortex

The long scale applies to Figure 6; the short scale to all other figures.

FIG. 1. *Halimeda fragilis*

FIG. 2. *Halimeda micronesica*

FIG. 3. *Halimeda bikinensis*

FIG. 4. *Halimeda scabra*

FIG. 5. *Halimeda gigas*

FIG. 6. *Halimeda opuntia*

FIG. 7. *Halimeda tuna*

FIG. 8. *Halimeda macrophysa*

FIG. 9. *Halimeda gracilis*

FIG. 10. *Halimeda cuneata*

FIG. 11. *Halimeda discoidea*

FIG. 12. *Halimeda lacrimosa*

FIG. 13. *Halimeda lacunalis*

FIG. 14. *Halimeda taenicola*

FIG. 15. *Halimeda simulans*

FIG. 16. *Halimeda monile*

FIG. 17. *Halimeda macroloba*

FIG. 18. *Halimeda stuposa*

FIG. 19. *Halimeda cylindracea*

FIG. 20. *Halimeda favulosa*

FIGS. 21–24. *Halimeda incrassata.* Figures 21–22, two stages in the ontogeny of a segment. Figure 21, nodal medullary filaments united into a single group, the filaments communicating by pores. Figure 22, an early stage in the extension of the medullary filaments from the node of a young segment. Figure 23, section from a mature segment. Figure 24, from a basal segment.

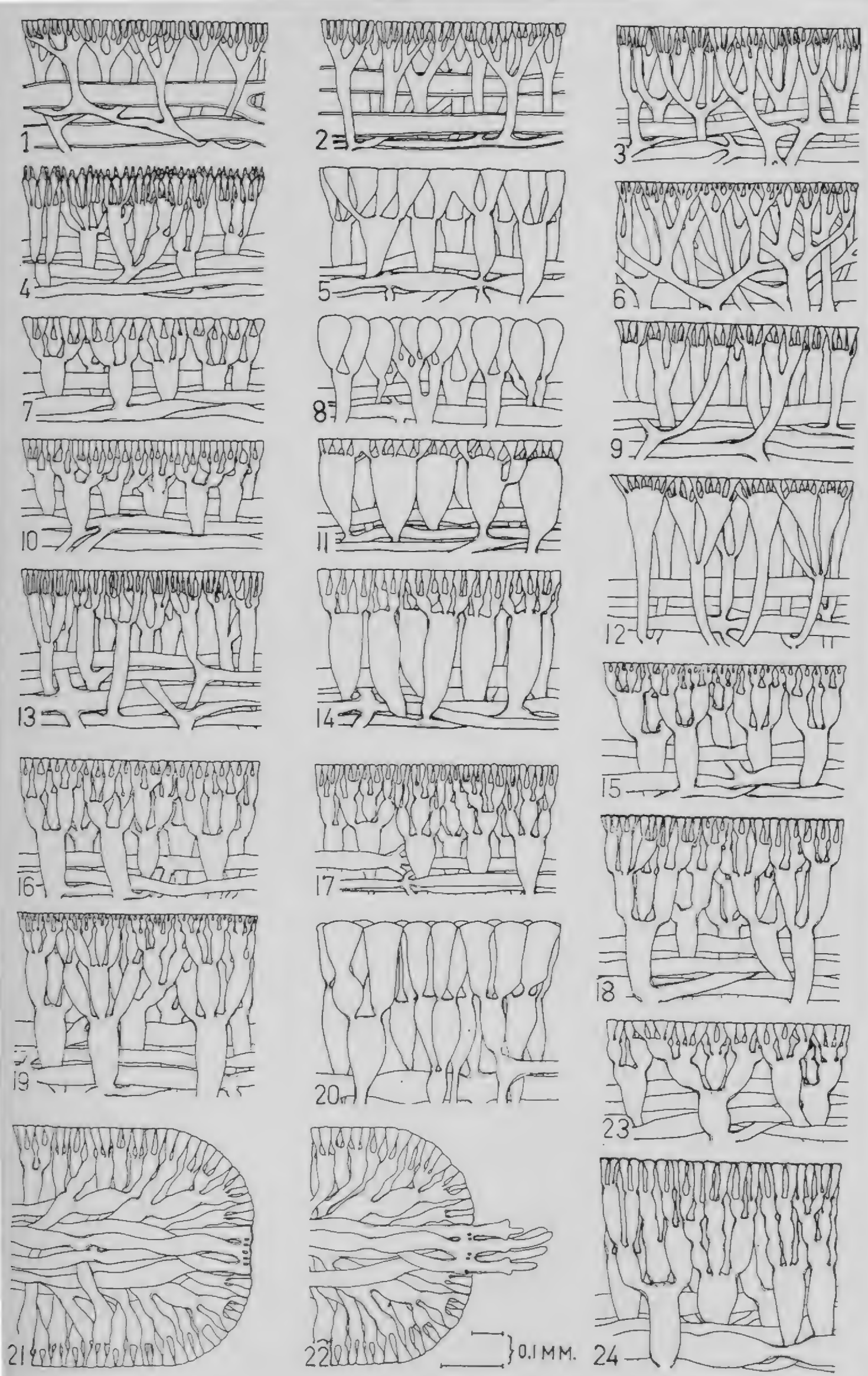
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PLATE 7

Organization of the Medullary Filaments at the Node

The long scale applies to Figure 11; the short scale to all other figures.

FIG. 1. *Halimeda fragilis.* Nodal medullary filaments remain separate and the wall thickening is generally quite pronounced.

FIG. 2. *Halimeda gracilis.* Extended fusion in pairs.

FIG. 3. *Halimeda opuntia.* Short fusion in pairs.

FIGS. 4–6. *Halimeda lacrimosa.* Types of nodal medullary filament behavior commonly encountered in this species. Figure 4, extended fusion in pairs. Figures 5–6, combinations of short and extended fusion, with two filaments rather than three or four resulting from the union of three and four filaments, respectively.

FIG. 7. *Halimeda cuneata.* Nodal filaments fuse in twos and threes, the units being densely entangled. The cushion segment with its cortex, and the uncorticated stalk region composed of torulose medullary filaments are shown above the region of fusion.

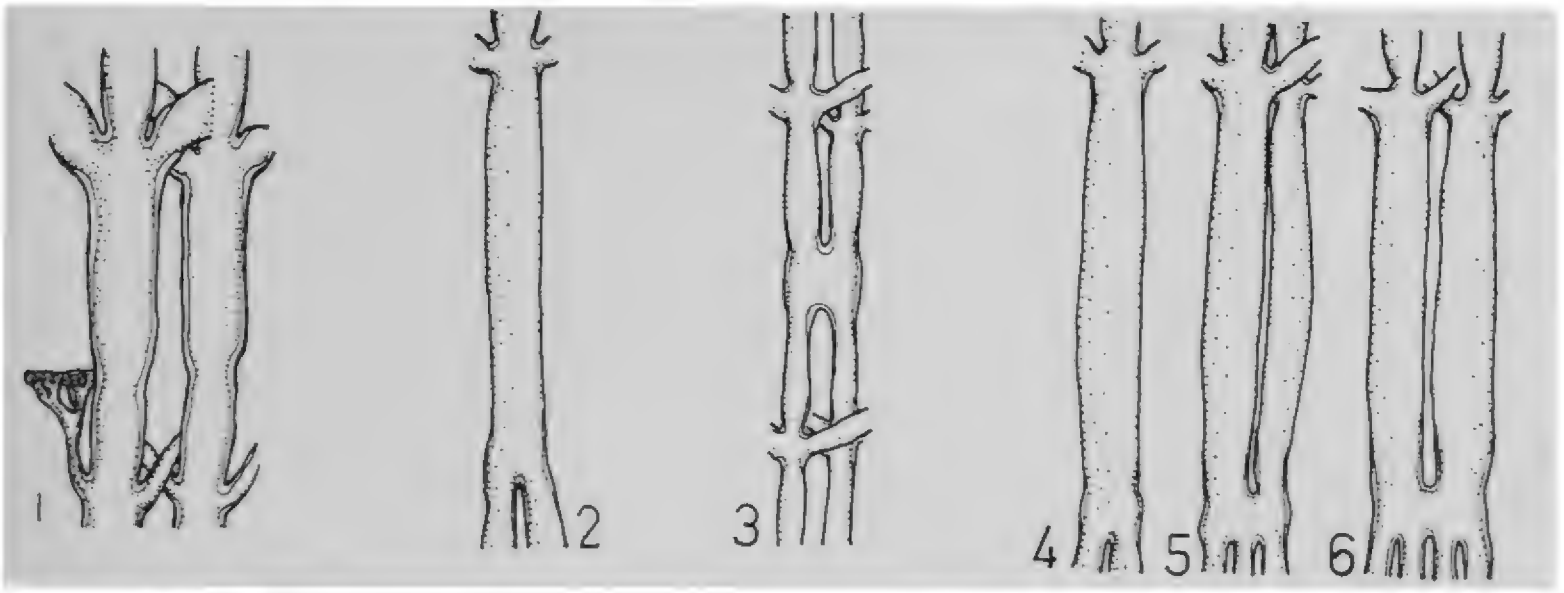
FIG. 8. *Halimeda lacunalis.* Lateral attachment of fused units which show extended fusion in pairs.

FIGS. 9–10. *Halimeda discoidea.* Figure 9, extended fusion in twos. Figure 10, short fusion in twos and threes.

FIG. 11. *Halimeda stuposa.* Transverse section through a node showing the fusion disk which is composed of united medullary filaments communicating by pores. The mode of fusion is similar to that illustrated in Figure 13. (The thick walls typical of the peripheral utricles for this species have been omitted.)

FIG. 12. *Halimeda monile.* Small groups of firmly fused filaments are united into larger groups by narrow tubes which sever relatively easily. A modification of the nodal filament behavior illustrated in Figure 13 is represented.

FIG. 13. *Halimeda cylindracea.* The medullary filaments unite into a large group for a short distance. Adjacent filaments communicate through thick-walled pores.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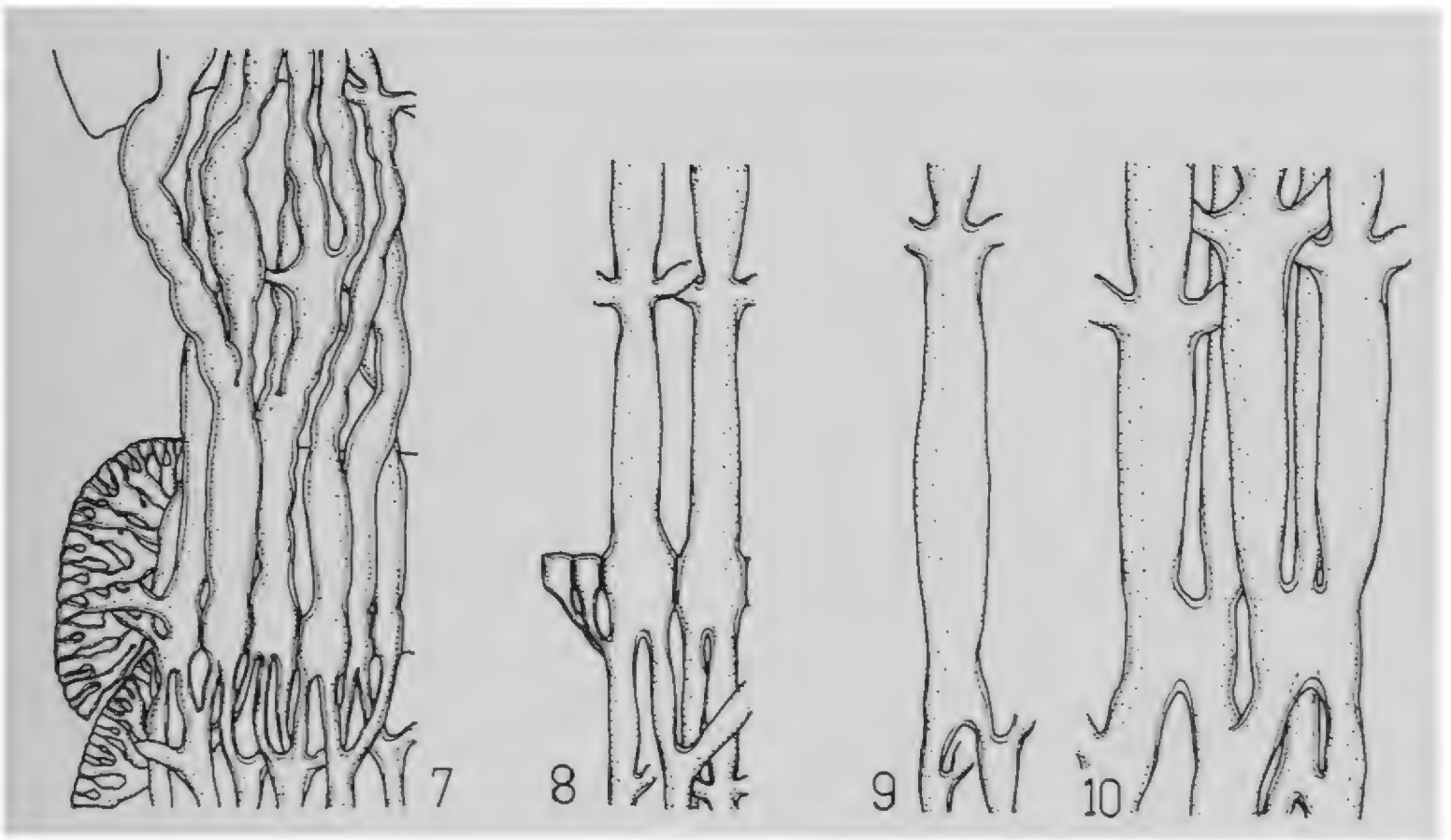
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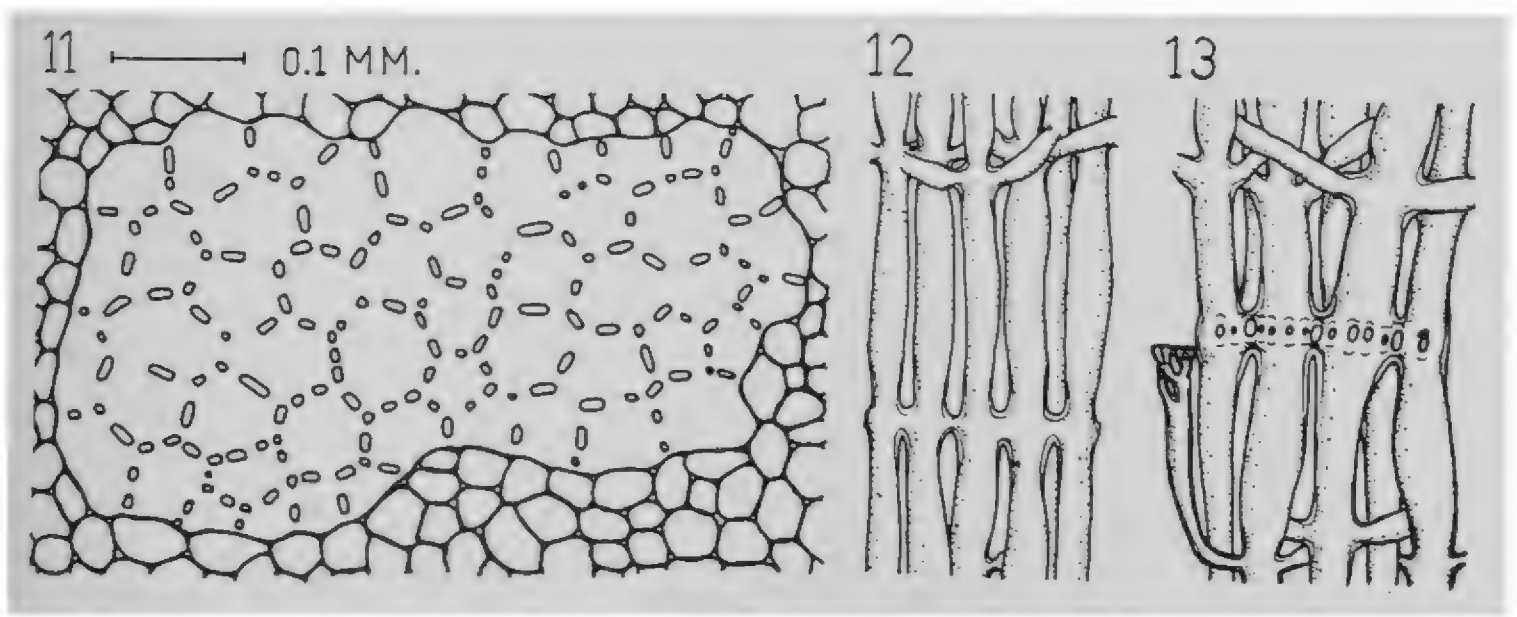
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PLATE 8

The upper scale applies to Figure 1 only.

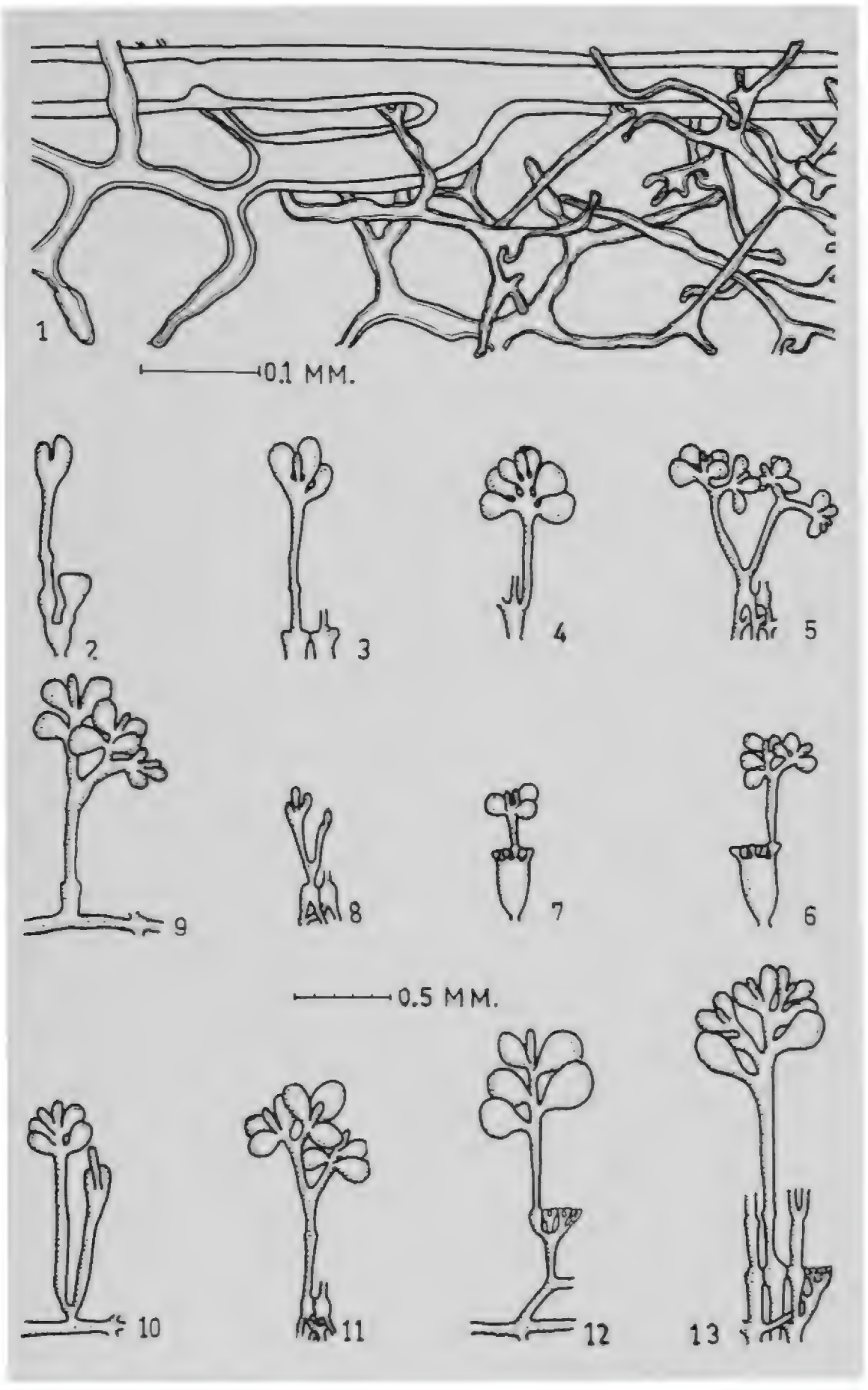
FIG. 1. *Halimeda fragilis*, rhizoidal filaments. The smaller filaments are often rather tightly entwined around the larger ones.

FIGS. 2–4. *Halimeda favulosa*. Stages in the development of gametangia. Figure 2, gametophore arising from a utricle. Figures 3–4, gametophores arising from medullary filaments.

FIGS. 5–8. *Halimeda discoidea*. Stages in the development of gametangia. Figures 5, 8, gametophores arising from medullary filaments subsequent to their fusion in pairs. Figures 6–7, gametophores arising from utricles.

FIGS. 9–11. *Halimeda scabra*. Stages in the development of gametangia. Figures 9–10, gametophores arising from medullary filaments. Figure 11, gametophore arising from medullary filaments subsequent ot their fusion in pairs.

FIGS. 12–13. *Halimeda monile*. Figure 12, gametophores arising from a utricle. Figure 13, gametophore arising from a medullary filament.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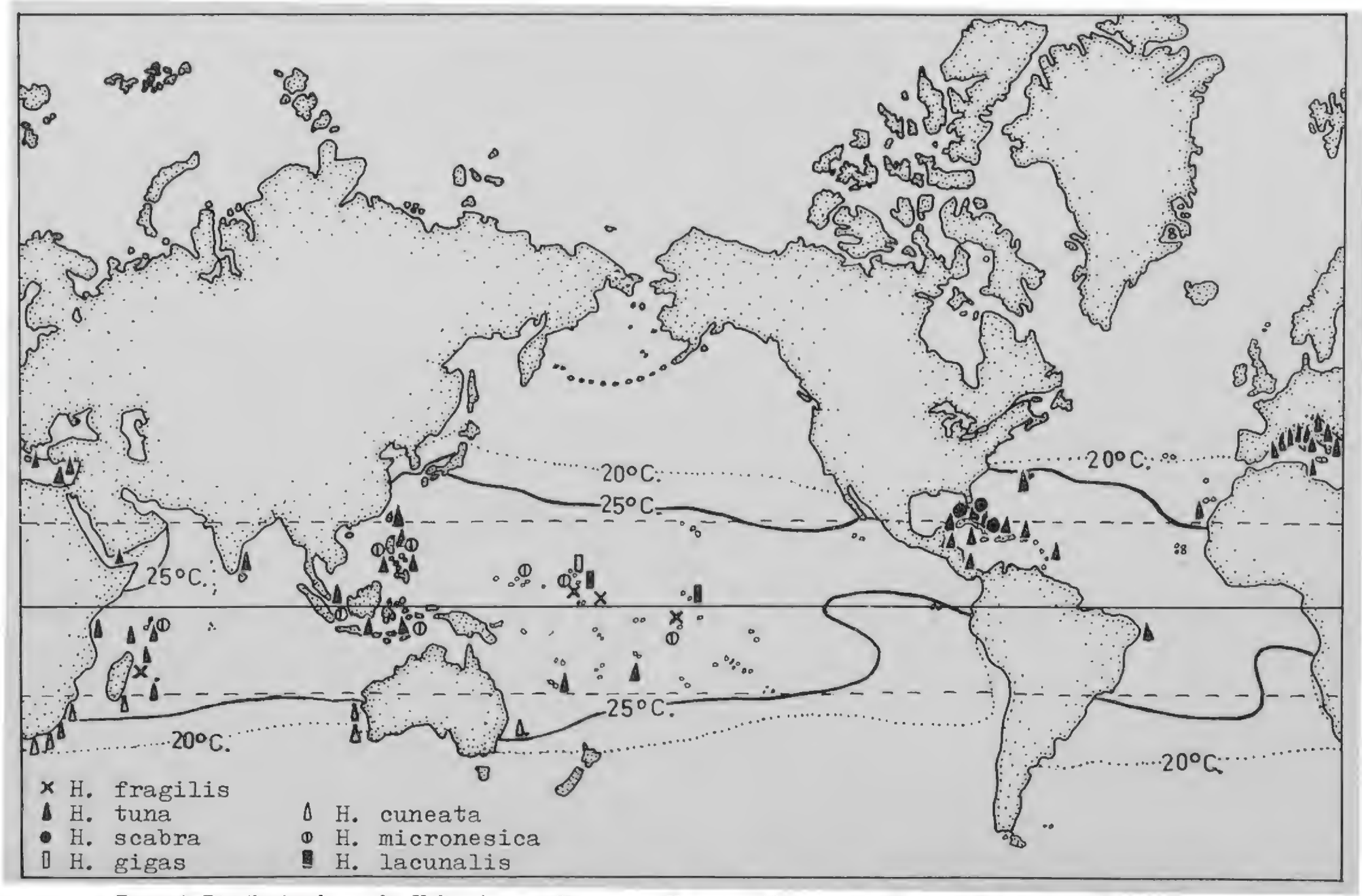

PLATE 9. Distributional map for *Halimeda tuna, H. cuneata, H. scabra, H. lacunalis, H. gigas, H. micronesica,* and *H. fragilis*.

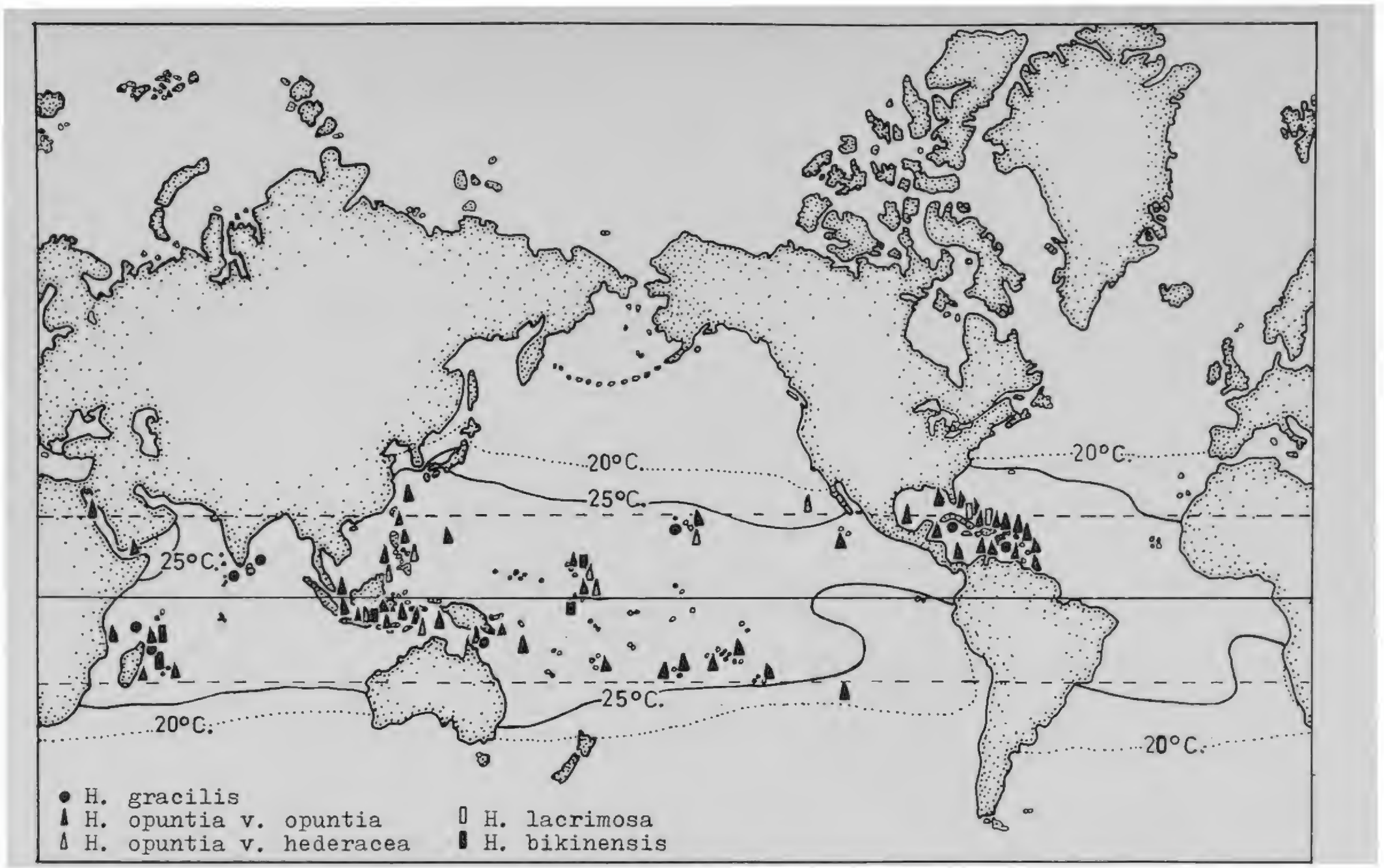

PLATE 10. Distributional map for *Halimeda opuntia, H. gracilis, H. lacrimosa,* and *H. bikinensis.*

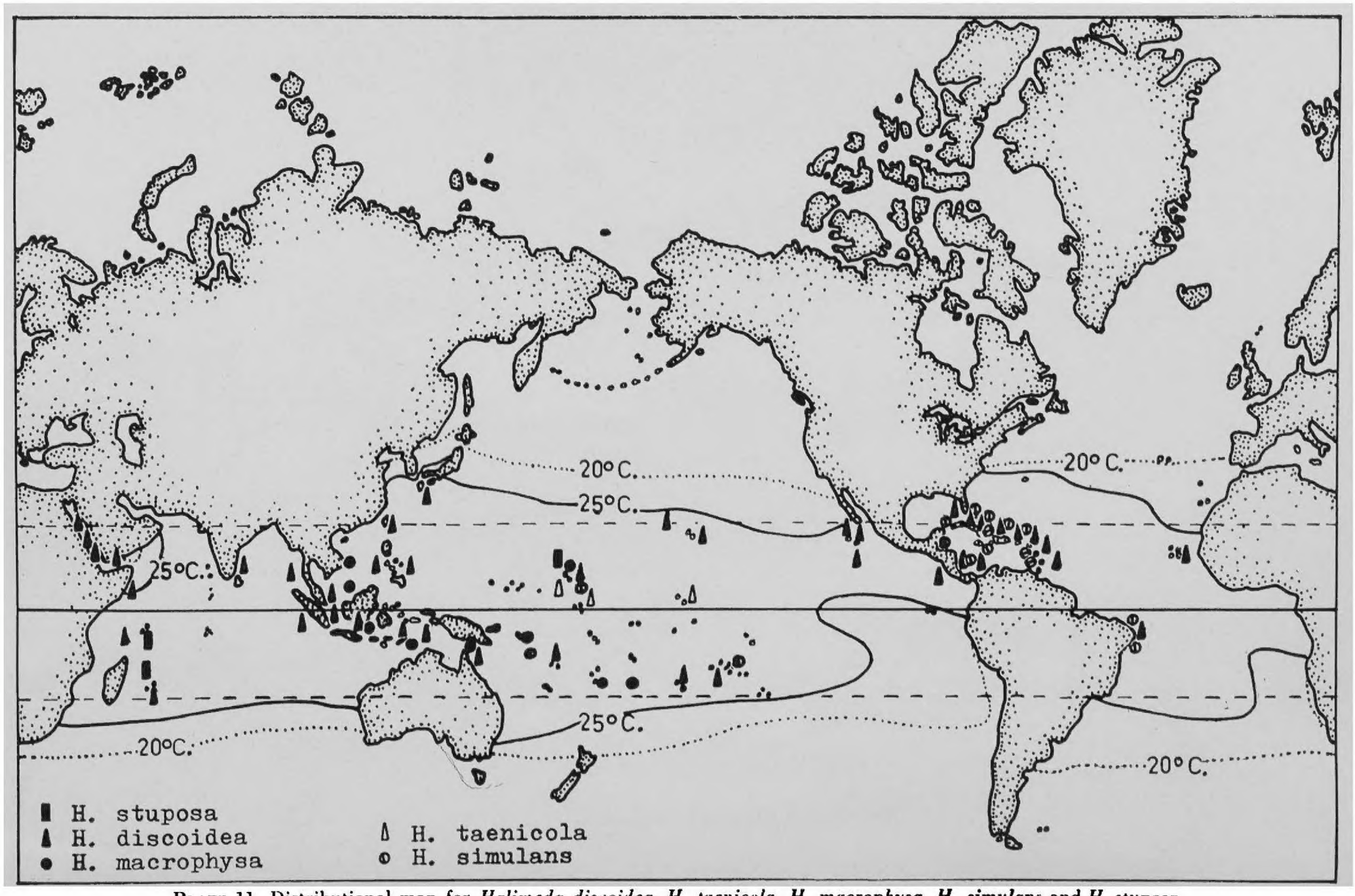

PLATE 11. Distributional map for *Halimeda discoidea, H. taenicola, H. macrophysa, H. simulans* and *H. stuposa.*

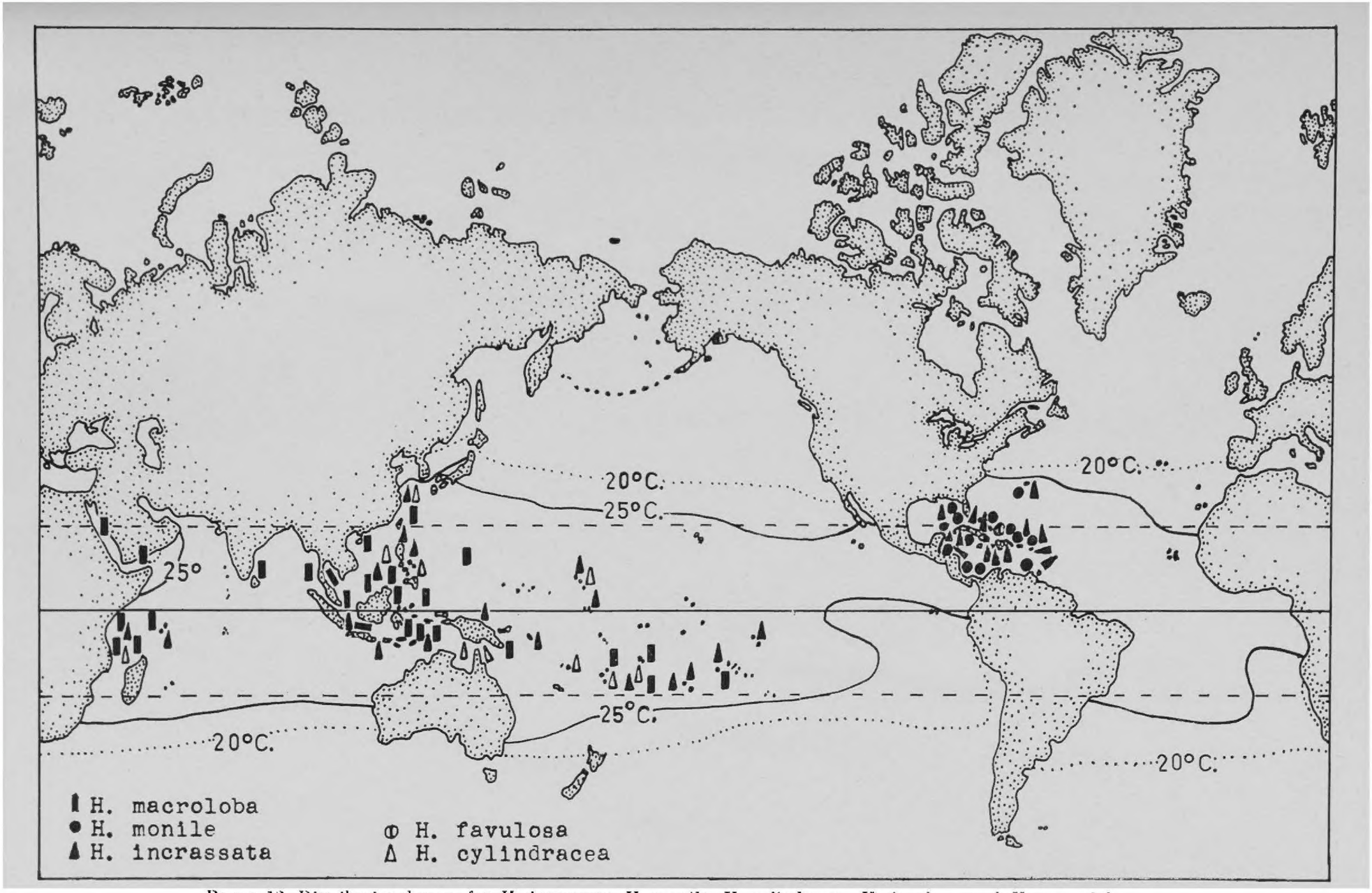

PLATE 12. Distributional map for *H. incrassata, H. monile, H. cylindracea, H. favulosa,* and *H. macroloba.*

ALACRAN REEF, CAMPECHE BANK, YUCATAN, MEXICO

INTER-REEF SEDIMENTS

SHALLOW INNER REEFS, FLATS, PATCH REEFS, & PINNACLES

SHALLOW SAND BANKS AND BARS

DEEP OUTER CORAL REEFS

SEAWARD SLOPE OF OUTER REEF

CAMPECHE BANK

SAND ISLANDS

12 DEPTH IN FEET. HOSKIN'S LEAD LINE SOUNDINGS, 1959

DEC'L. 7° 41" E, 1959

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KILOMETERS

L. S. KORNICKER
C. M. HOSKIN
H. COMPTON
R. CANN

Kornicker, L. S., F. Bonet, R. Cann, and C. M. Hoskin 1959. Alacran Reef, Campeche Bank, Mexico. Publicatic .f the Institute of Ma ne Scien